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Transactions of the Academy of Science of St. Louis

Volume XXVI, No. 1

THE LIZARDS OF KANSAS

Charles E. Burt

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THE LIZARDS OF KANSAS*

CHARLES E. BURT

Considerable work has been done on the lizards of Kansas, but it is scattered through various publications and manuscripts, and there is evident need for consolidation and further research.

Three papers of primary interest to students of the herpetology of Kansas are those of Dr. F. W. Cragin (1881, 1884, and 1885), in which fifteen species of lizards were listed from the state. After making extensive collections during the summer of 1916, Mr. Victor H. Housholder prepared a thesis on the "Lizards and Turtles of Kansas,"** and during the same year Dr. Edward H. Taylor completed a manuscript study of the "Lizards of Kansas."** The author has recently written an article on "The Insect Food of Kansas Lizards, with Notes on Feeding Habits," which is soon to appear in the recently established Journal of the Kansas Entomological Society. Since full accounts are given in it, only summary sentences of the feeding habits of each species are presented below.

This present work was done at the Kansas State Agricultural College during the years 1924 to 1927 with the following objectives in view: (1) The determination of the species of Kansas lizards, (2) The study of their taxonomy and variation, (3) The preparation of a key for their identification, (4) The preparation of an outline of their distribution, with an analysis of the ecological factors which influence it, and (5) The presentation of a study of their habitats and habits.

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*Contribution No. 99 from the Department of Zoology of the Kansas State Agricultural College.

**These works were produced independently at the Kansas University Museum.

Over 1,700 specimens of Kansas lizards have been examined by the writer during the progress of this study. These have been taken from 83 of the 105 counties of the state. Correspondence with many Kansas persons has yielded a large reward of specimens, and in addition the author has personally collected 275 Kansas lizards, including representatives of ten species and subspecies, many of which are from hitherto unworked areas.

Good discussions of collecting and preserving methods, which have been found useful, are given by Stejneger (1891), Ruthven (1912), and Loding (1922).

Reports of lizards, whether in the literature or not, have always been considered, but have not been accepted unless the specimens are in existence and the data of collection are thought to be without the possibility of error. The taxonomy used is after Stejneger and Barbour (1923) unless otherwise stated. The literature has been consulted extensively for descriptions of Kansas lizards, and these have been checked, and at times modified, with the aid of specimens. Thus, the descriptions presented in this paper are the summary of data taken directly from Kansas material.

The study of variation has included the taking of measurements on all available specimens, and units of the metric system have been used for their expression. Important characteristics of the individual species, such as the interorbital scutellation of *Crotaphytus collaris*, or the barring on the sides of *Holbrookia maculata maculata*, have also been given considerable attention.

This work was done at the suggestion and under the general direction of Dr. Minna E. Jewell of the Kansas State Agricultural College, to whom the writer wishes to express his grateful appreciation for many helpful suggestions and criticisms. Thanks are extended par-

ticularly to Dr. Edward H. Taylor of Kansas University for the loan of his unpublished work on "The Lizards of Kansas" with the permission to use extracts from it* in the preparation of this paper, for complete data on the lizard collections of the Kansas University Biological Survey of the summer of 1926, and for his hearty co-operation throughout the progress of this study; and to Mr. Victor H. Housholder, formerly of Kansas University, for the loan and permission to use extracts from his unpublished manuscript on "The Lizards and Turtles of Kansas"*; also to Dr. Frank N. Blanchard of the University of Michigan for the checking of identifications of lizards which were referred to him; to Dr. L. Stejneger and Miss Doris M. Cochran of the United States National Museum for some helpful identifications, opinions, and reports; and to Mrs. Helen T. Gaige of the Museum of Zoology of the University of Michigan for aid in the identification of certain specimens of *Eumeces*.

Through the courtesy of Mr. C. D. Bunker of the Kansas University Museum a large part of the data used in the preparation of this work were secured from the excellent collection of over 1,000 specimens of Kansas lizards preserved there. Mr. Howard K. Gloyd has kindly loaned the lizard collection of Ottawa University, Mr. L. D. Wooster that of the Kansas State Teachers' College of Hays, the Rev. Felix Nolte that of St. Benedict's College, and Dean Emil O. Deere that of Bethany College. The United States National Museum has been very helpful in loaning specimens of the rarer species of lizards.

The author wishes to express his appreciation to his wife, May Danheim Burt, with whom he has discussed much of this work, for assistance in the taking of data

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***All items that are quoted from these sources are indicated by the use of the author's name and the designation, "(Unpublished)".**

on specimens of lizards which he examined at the Kansas State Agricultural College; and to his cousin, Mr. W. H. Burt, formerly of the Kansas University Museum, who kindly assisted in a similar way while the writer was studying the lizards preserved there.

The writer feels very grateful to Dr. Robert K. Nabours of the Kansas State Agricultural College for his continual encouragement and co-operation during the time occupied by this study, and also for furnishing facilities in making exchanges.

A large number of persons have contributed specimens of lizards to Kansas museums, but the list is too large and incomplete to be reproduced here. There are a number of persons who have been very kind in sending the writer both specimens and data, and to these he is extremely grateful. Among these, aside from those who have already been mentioned, are F. F. Crevecoeur, H. J. Harnly, Ivan R. Burket, A. J. Cheatum, L. M. Clausen, Frank W. Jobes, H. H. Schwardt, Harry G. Walker, Stephen T. Egan, A. P. Williams, T. E. White, Leonard Montgomery, Gerald G. Grout, W. J. Robinson, Robert Kingman, William R. Thompson, Kathlene Margaret Thompson, Verl Fink, Paul White, A. R. Miller, and Floyd Pauley.

A Key to the Species of Lizards Definitely Reported from Kansas

1. **Four legs present; lateral fold absent..... 2**
   Legs absent; lateral fold present..... ..
   Anguidae. *Ophisaurus ventralis* (Linné).p. 36
2. **Femoral pores present or head with conspicuous spines..... 3**
   Femoral pores absent and head without spines.....Scincidae. 9
3. **Lateral scales not abruptly smaller than ventrals; ventrals in numerous series .....Iguanidae. 4**
   Lateral scales abruptly smaller than ventrals; large ventrals in eight longitudinal series..... ..
   Teiidae, *Cnemidorphorus sexlineatus* (Linné).p. 38
4. **Body flattened and with many horny tubercules or spines; tail less than forty per cent of total length.....*Phrynosoma.* 5**
   Body not noticeably flattened; horny tubercules and spines absent; tail over forty per cent of total length..... 6

5. Two rows of marginal spines present along sides..... ..
P. cornutum (Harlan).p. 27
One row of marginal spines present..... ..
P. *douglassii ornatissimum* (Girard).p. 32
6. Ear opening present; upper labial scales not oblique and not overlapping 7
Ear opening absent; upper labial scales oblique and overlapping ....
Holbrookia maculata maculata (Girard).p. 11
7. Dorsal scales smooth; black collar present..... ..
Crotaphytus collaris (Say).p. 5
Dorsal scales keeled and converging to a point posteriorly; black collar absent.....*Sceloporus* 8
8. Wavy dark brown cross bars present on sides and back..... ..
S. undulatus undulatus (Latreille).p. 19
Cross bars restricted; small dark brown spots usually present on sides.....*S. undulatus thayerii* (Baird and Girard).p. 16
9. Lower eyelid with transparent central part; body bronze above, cylindrical; limbs minute.....*Leiolopisma laterale* (Say).p. 45
Lower eyelid scaly; body not noticeably cylindrical; limbs of moderate size .....*Eumeces* 10
10. Lateral scale rows extending parallel to dorsal rows..... 11
Lateral scale rows extending diagonally from ventro-lateral to dorso-lateral surface..*Eumeces obsoletus* (Baird and Girard). p. 58
11. Back with seven or more narrow light stripes, and nine or more dark bands.....*E. multivirgatus* (Hallowell).p. 56
Back with fewer light stripes and dark bands..... 12
12. Body blackish, with five prominent light lines, the center one forking on the head.....*E. fasciatus* (Linné). Young to adult in primary stage of development.....p. 51
Body with four prominent light lines, four faint lines, or none 13
13. Body with two prominent light lines and two broad dark bands on each side.....*E. septentrionalis* (Baird).p. 63
Body with two light lines on each side, prominent or not; these bordering a broad, dark band of solid color; or with lines absent 14
14. Lines absent; cheeks reddish or brown; general coloration light. *E. fasciatus* (Linné). Aged adult in tertiary or last stage of development .....p. 51
Lines present; general coloration usually somewhat darker.... 15
15. Scales of wide mid-dorsal band with perceptible light and dark areas, not unicolor.....*E. fasciatus* (Linné). Adult in intermediate stage of development.....p. 51
Scales of wide mid-dorsal band not with light and dark areas, but unicolor; the band black to brown.....
E. anthracinus (Baird).p. 49

A LIST OF THE SPECIES OF LIZARDS DEFINITELY KNOWN TO INHABIT THE STATE OF KANSAS

Crotaphytus collaris (Say)*

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*The data upon which the writer's views of the synonomy of this species are based will be presented in his forthcoming work on "The Synonomy, Variation and Distribution of the Collared Lizard, *Crotaphytus collaris* (Say)", which is to be published in the Occasional Papers of the Museum of Zoology of the University of Michigan.

Collared Lizard, Mountain Boomer, Black Shouldered Lizard, Bull Lizard, Gray Nellie.

Description.—Head large and sub-triangular; body thick; tail long and tapering to a point; supraocular scales usually small, excepting for a few enlarged ones near the center; supraocular area rising above interorbital area; ear opening large and prominent, with an anterior denticulation; tympanum exposed; one gular fold well developed, three sometimes present; labials not oblique or overlapping; lower series larger than upper series.

All body scales finely granular; scales of back and sides about equal in size; ventrals larger; femoral pores distinct, well developed, with white, brown, or black centers, enlarged in males, small in females; number, from fourteen to twenty-five; back part of mouth cavity black; males with one or more pairs of enlarged post-anal plates; females usually with even transverse scutellation behind anus.

Coloration varies; colors well defined in nature, but fade to dull shades in captive specimens; coloration lighter at high temperatures and darker at lowered temperatures*; ventral color varies from a medium brownish to an immaculate white, through various shades of greens, grays, and blues; Kansas specimens without black or brown loin patches; dorsal ground color varies from blackish gray to light bluish gray; usually with pale dots which have no definite order of arrangement; light colored bars extending transversely across the dorsal surface in certain specimens; back often with scattered flecks of brown, orange or reddish; lower jaws

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*Franklin (1913) found that "During the cooler hours of the day these lizards were a dark dirty gray, but when the air was warm and the lizards became more active, the color changed to a bright emerald green."

occasionally with a pattern of alternate white and gray transverse bars, giving a "tiger design"; upper head scales usually green or brownish olive with the coloration becoming more intense as the median line is approached.

Double black collar on shoulders, not extending ventrally in Kansas specimens; both bars of collar usually broken dorsally; back and tail of same general coloration; tail much more blotched and sometimes with ringed appearance; color duller in young than in adults; large males sometimes with highly colored gular region of orange or yellow and much of the rest of the body blue or green; other males and always females, duller.

During the fall of 1925 the writer collected, and observed the coloration upon, over forty young specimens, all of which showed the dull coloration characteristic of the female. The colors of all forms are deeper after the skin is shed, and those of the adults, also, at the spring of the year during the mating season.

In 275 specimens from Kansas the number and arrangement of the scales between the orbital areas has been found to be as follows: specimens with two distinct rows, 28 or 10.2 per cent; specimens with two of these paired scales fused to one single scute, 115 or 41.9 per-cent; specimens with four fused to two singles, 121 or 44.0 per cent; specimens with six fused to three singles, 10 or 3.6 per cent; and specimens with eight fused to four singles, 1 or 0.3 per cent. This indicates that the interorbital scutellation of Kansas individuals presents, essentially, a condition of two rows, excepting for a few fused scales which make a single row for a short distance.

A summary of the study of 300 Kansas specimens is given below. *Measurements are given in millimeters,*

thus: "*Minimum—maximum* (*mode*)" *in this and in all of the following summaries.* Length of body, 38-111 (81-90); length of tail, 57-210 (151-165); total length 98-309 (221-240); width of head, 9-29 (18-20); length of tail as percentage of body length, 57.1-72.5 (64.1-66); width of head as percentage of body length, 20.0-30.0 (22.1-24).

Ellis and Henderson (1913) have listed this species as reaching the total length of 380 millimeters, which is greatly in excess of the length of the largest Kansas specimen examined by the writer.

Habitat and Habits.—Cope (1866) gave the habitat of this species as, "Sand, logs, among brush, etc."—Stejneger (1893) found it to be "Evidently an inland desert form of the Upper Sonoran life zone."—Van Denburgh (1897) found that this reptile is a lizard of the desert, but that it does not seem to live on its lower levels, preferring the more mountainous regions between the altitudes of 4,500 and 6,500 feet. Taylor (1912) wrote of Humboldt County, Nevada, specimens, stating that "Eleven were taken near Big Creek Ranch at altitudes ranging from 4,800 to 5,400 feet. We look in vain for this species in the open desert and on certain of the lower slopes of the mountains. All but one of the specimens were collected on the top of a steep sided rocky ridge." Richardson (1915) stated that "The lizard was found only on hillsides amid deposits of tufa and outcroppings of volcanic rock at an elevation of 4,500 feet." In Kansas, collared lizards have been collected only between the altitudes of 800 and 2,200 feet, though there are points in western Kansas with an altitude of 4,000 feet. Bentley (1919) wrote that specimens were usually found in Nye County, Nevada, "On the large, flat rocks of a steep hillside."

Dr. Ivan R. Burket of Ashland, Clark County, Kansas,

wrote in May, 1925, that "A specimen ran into a hole on our golf course, and to obtain it, I had to dig it from its shelter." Prof. L. D. Wooster of Hays has stated that he found collared lizards along the rocky hillsides which border the Smoky Hill River in Ellsworth County. The writer has found this species to be almost always near rocky ledges, especially along the brows of hills. The flat, loose-lying, limestone rocks of the rolling prairie country are very characteristic of its habitat. On warm days of the spring, summer, and fall, this reptile may often be found sunning itself on a rock or boulder or going about in search of food. The winter is spent in hibernation under the rocky ledges.

A variety of Kansas habitats are known for this species. In Riley County it has often been found under hillside rocks, around rock fences, and in rock quarries. Also, several specimens have been observed along the banks of the wooded Wildcat stream, west of Manhattan, where two of these little animals were found very close to water. Along a low, flat, barren, rocky, sandy ledge, which was exposed to the hot May sun of Rush County, a specimen was taken. Though the species is more frequently found near wooded slopes, this particular specimen was far from trees.

Very few notes have appeared which deal with the breeding habits of the collared lizard. Hallowell (1856) dissected a large female and found eight large eggs. Strecker (1910) stated that "The eggs range in number from four to twenty-four, and are deposited in loose sand to a depth of four or five inches." Ditmars (1915) recorded the deposition of a total of twenty-one eggs by a large female. Taylor (unpublished) found the egg number to be from five to seven, stating that "They are deposited at the end of shallow tunnels immediately be-

low large, flat rocks. The passageway near the eggs is then stopped up by the female with closely packed earth, and the young must dig their way out after hatching.'' A Riley County specimen which the writer opened contained seven eggs. Another which was transported to Cheboygan County, Michigan, early in the summer of 1927 laid two eggs on June 26, one on July 1, two more on July 2, and finally four others on July 4, a total of nine eggs in nine days.

The food of *Crotaphytus collaris* consists, chiefly, of the larger insects, particularly grasshoppers and crickets.

Distribution in Kansas.—Kansas specimens that might be identified as the ''*baileyi*'' type have always been found in co-extensive distribution with the ''*collaris*'' type. The collared lizard has been taken in the eastern two-thirds of the state only. It has generally been found about rocky formations which cover a considerable area, and has usually been absent from small outcroppings of rock. This, together with the fact that it has not been collected in large cultivated areas, such as are found in Rice, Barton and Brown counties, would tend to indicate that it is not a species highly resistant to the encroachments of man upon nature, and as agricultural methods become more intensive and more ground is tilled in Kansas the area of its distribution will probably be constantly decreased. Although the collared lizard is said, by various writers, to be a desert form, the author has not found it in the drier situations of Kansas, even though rocks were there in abundance. It is usually found where there is considerable moisture, typically at the upper edge or above the woods which are found near streams, and the dry condition which is presented by the climatic cycle of western Kansas may help

to restrict its range from that area. Neither the large chalk beds of Trego and Gove counties, nor the great sandy areas of the state, as those in Reno and Stafford counties, have yielded specimens of the collared lizard. Northeastern Kansas apparently does not present favorable geological conditions for its dispersal, and too, it is

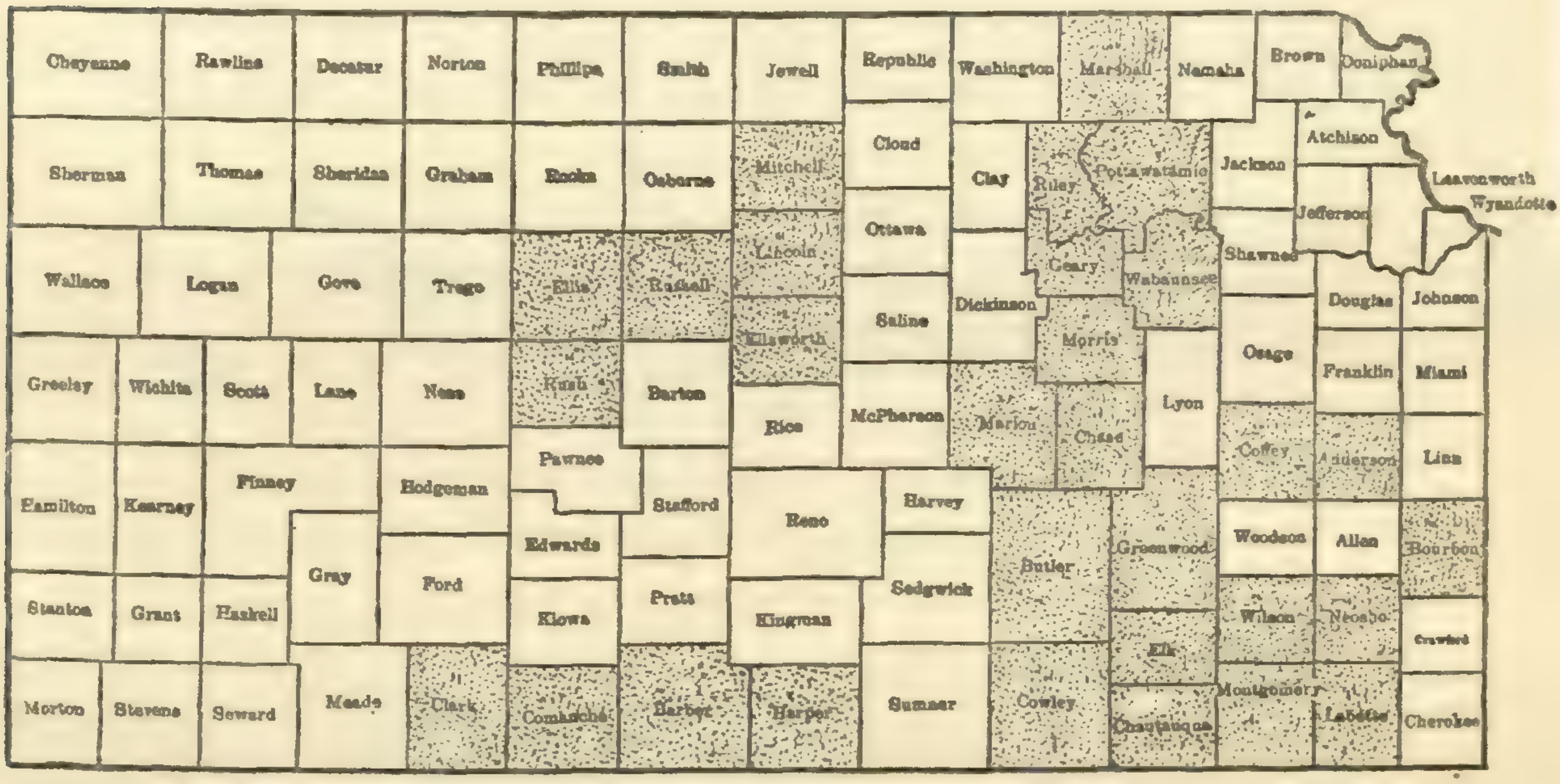

Fig. 1. Distribution of *C. collaris* in Kansas as indicated by the county reports.

an area characterized by a dense agricultural population.

Holbrookia maculata maculata. (Girard).
Holbrook's Sand Swift, Spotted Lizard,
Cactus Lizard.

Description.—Head broad and short, convex; widest in orbital region; muzzle broad and rounded; neck thick; body rather stout and depressed with tail tapering rapidly to a point; tail thick at its base; ear opening absent; six oblique and imbricate upper labials; strong superciliary ridge above eye; supraocular region not elevated above superciliary ridge; head scales moderately tuberculate; dorsal scales small, finely granular,

and somewhat tuberculate in large specimens; ventrals decidedly larger; enlarged post-anal plates present in males only.

Coloration not highly variable; ventral parts immaculate white, with or without a "tiger design" of slate colored bars on the chin; dorsal ground color ashy gray, with two rows of dark blotches extending from the region posterior to the head to well upon the tail, varying in series, anterior to posterior, from ten to fourteen in number; median line distinct and free from blotches; a row of lateral blotches on each side, usually not sharply defined, but distinctly visible; subcaudal black spots never present; from two to four black latero-ventral bars on each side of abdomen; lateral aspect of the belly sometimes bluish; otherwise, the ground color of the sides varies from light yellowish through different shades of orange to dull reddish.

By the examination of 148 specimens of *H. maculata maculata* from Kansas, it was found that the black bars on the right side numbered from two to four units, as follows: with two bars, 104 specimens; with three bars, 38 specimens; with four bars, six specimens. There is sometimes the same number of bars on each side of this lizard, two being the most common, but frequently there is a variation, three on one side and two on the other occurring most often. Schmidt (1922) found in a series of nineteen females from Colorado that ten had two spots on each side, four had two spots on one side and three on the other, five had three spots on each side, and one had three on one side and four on the other.

In order to study the variation in size and proportion of this lizard 175 Kansas specimens have been measured. Unfortunately the writer failed to sex a large proportion of them, so sexual dimorphism cannot be fully treated.

A summary of the data follows. Length of body, 20-61 (45-60); length of tail, 17-76 (36-45); total length, 38-132 (91-100); width of head, 4.5-11 (8-9); length of tail as percentage of total length, 39.9-58.3 (44-46); width of head as percentage of body length, 13.0-22.9 (18-20).

In his key to the species of *Holbrookia*, Schmidt (1921, 1922) separated *H. maculata maculata* from other lizards of the genus by the character, "Tail shorter than body in the female, usually also in the male." To test this distinction, 32 specimens, males and females in equal numbers, were selected and measured. The results, expressed in terms of length of tail as percentage of total length, are as follows:

Males: Range, 44.0 to 58.3 per cent; average, 49.0 per cent.

Females: Range, 41.0 to 49.3 per cent; average, 45.0 per cent.

This indicates that Schmidt's distinction holds universally for the females, but does not do so for the males. Twenty-nine or 18.5 per cent of the 175 specimens cited in the measurement table above had a tail length of over 50.0 per cent. Granting that they are all males, the probability of error (as indicated by this series) in the identification of a male of *H. maculata maculata* by Schmidt's key would be approximately 37.0 per cent.

All of the measurement figures given by other writers for this species fall, so far as known, within the ranges designated in this work.

There has been considerable question as to the possible presence of *H. maculata lacerata* in Kansas. Cope (1900, p. 293) reported it from Neosho Falls, Woodson County, on the basis of three specimens (No. 4693) in the collection of the United States National Museum. The examination of over 200 specimens of *H. maculata* from Kan-

sas has failed to reveal anything but the typical *H. maculata maculata.* No specimens have been found with subcaudal black spots, or without latero-ventral black bars. The specimens identified by Cope as *H. maculata lacerata* had previously been referred by Dr. Stejneger to *H. maculata maculata*, as stated by Schmidt (1922). Dr. Stejneger wrote to Mr. Housholder of Kansas University in 1916, stating that "So far as coloration of the upper parts is concerned, *H. maculata lacerata* is closely approached by three specimens from Neosho Falls, Kansas, and in regard to the lateral spots, it may be stated that they are present." Housholder (unpublished) borrowed these specimens from the United States National Museum and after examining them wrote that, "There are two distinct dark blue spots on the sides of each of the specimens, but no evidence of the transverse spots on the inferior surface of the tail; therefore, considering these facts, Dr. Stejneger's statement, and Bailey's (1905) restriction of this subspecies to Texas, I consider the identification of Cope's three Neosho Falls specimens as very doubtful, and the occurrence of *H. maculata lacerata* in the state as very unlikely." In view of the existing data the writer feels little hesitancy in witholding the subspecies, *H. maculata lacerata*, from the Kansas faunal list.

Habitat and Habits.—Little has been written about the natural habitat of this small lizard. Taylor (unpublished) found a great many specimens in the chalk country of western Kansas. Housholder (unpublished) found them rarely under rocks and other objects, unless they were driven there for safety. He has stated that "A specimen was captured while attempting to swim a riffle in a small river. It is very probable that the lizard was driven from the gravel at my approach, and had taken to the water as a means of escape."

The writer has usually found this lizard in the open sun in places with sparse vegetation. It lives in small holes in the sand or gravel and stays there during the night, and on cold and cloudy days. When disturbed by a collector it often escapes by running swiftly into plum thickets, which are numerous where it occurs in abundance.

Little attention has been given to the breeding habits of these sand swifts. Taylor (unpublished) found the egg number to be from six to eight. A specimen which was collected in Osborne County, late in July, 1926, contained seven eggs which measured about twelve by eighteen millimeters in size.

This species is a voracious feeder upon small insects, particularly small grasshoppers and bugs.

Distribution in Kansas.—The range of the spotted lizard in Kansas extends approximately over the western two thirds of the state. Although listed from Woodson, Wilson, Elk, and Butler counties, it is very uncommon in the southeastern part of the state and occurs there only in sandy areas. In McPherson County it was found on "Twin Mounds," which are two large sand and rock covered hills that rise above the prairie. The distribution of the lizard in that vicinity was very local. Its power to live in a small favorable area might help to explain its widespread distribution over isolated sandy places like those of southeastern Kansas mentioned above. In the sand dune region surrounding the salt marshes of Stafford County this subspecies is present in large numbers, and may be seen on warm days of the spring or summer running swiftly across open sandy places which are interspersed with small patches of vegetation. The chalk beds of Trego and Gove counties have yielded many specimens. In Ottawa County the writer found this

lizard in the center of a sandy wheat field. *Holbrookia maculata maculata*, and specimens of *Cnemidophorus sexlineatus* and *Sceloporus undulatus thayerii*, are practically the only lacertilian inhabitants of many of the counties of the western half of the state, and are the only specimens that have been taken from much of that area, including Trego, Gove and Stafford counties.

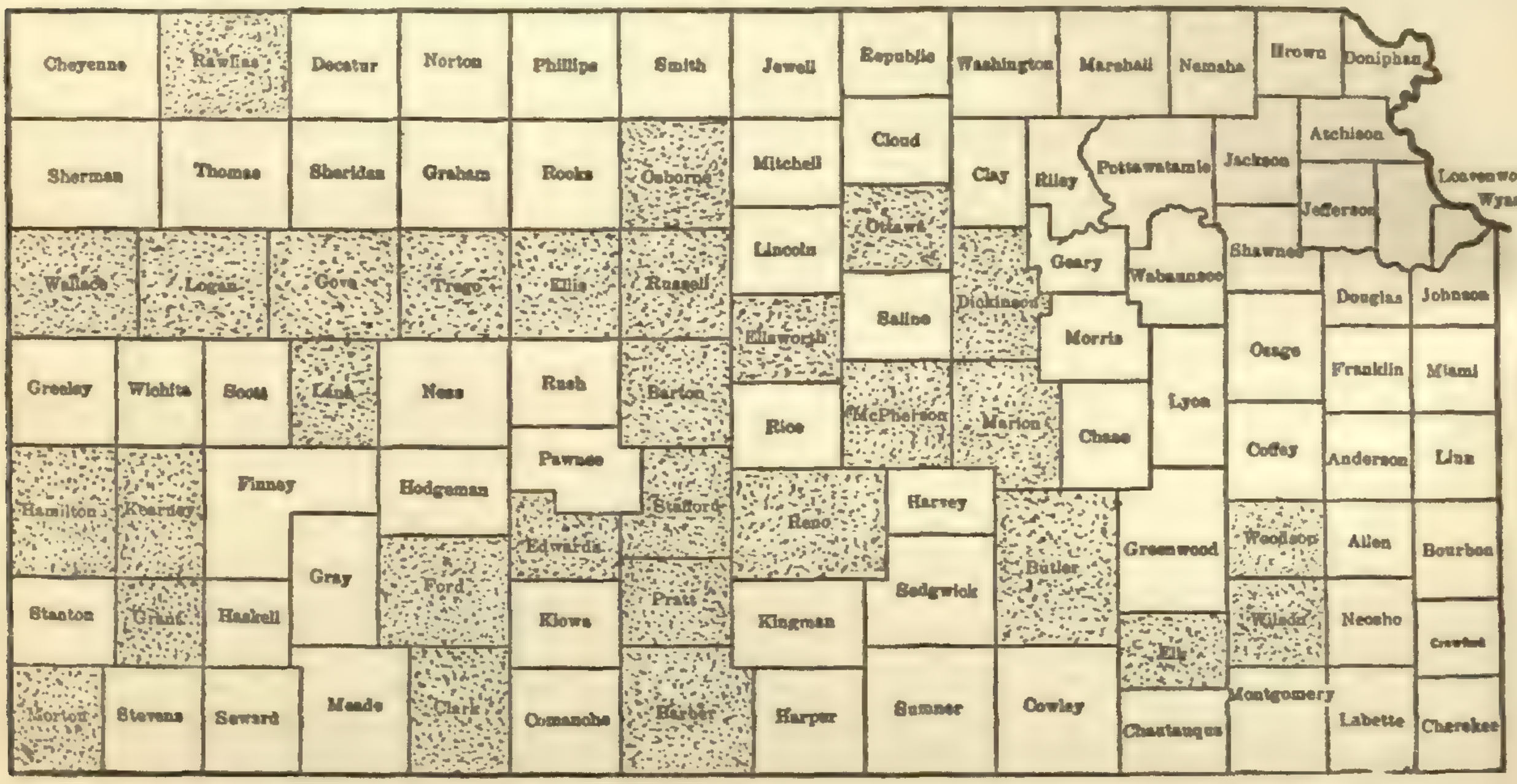

Fig. 2. Distribution of *H. maculata maculata* in Kansas as indicated by the county reports.

Sceloporus undulatus thayerii. (Baird and Girard).

Yellow-banded Swift, Striped Spiny Swift, Thayer's Alligator Lizard.

Sceloporus thayerii.—Baird and Girard, 1852, Proc. Acad. Nat. Sci. Philadelphia, 6:127 (type locality, "Indianola, on the Gulf of Mexico, San Antonio, Texas, El Paso del Norte, and as far westward as the Province of Sonora").

Sceloporus consobrinus.—Baird and Girard, 1853, Rept. Marcy's Expl. Red River, p. 237.

Sceloporus undulatus thayerii.—Cope, 1875, Bull. U. S. Nat. Mus., 1:49.

Sceloporus undulatus consobrinus.—Cope, 1900, Ann. Rept. U. S. Nat. Mus, for 1898, p. 377.

Sceloporus thayerii.—Cope, 1900, Ann. Rept. U. S. Nat. Mus. for 1898, p. 385.

Sceloporus consobrinus consobrinus.—Stejneger and Barbour, 1923, Check List N. Amer. Amph. Rept., p. 54.

Jones (1926) has shown that *S. thayerii* is the proper name for *S. consobrinus*, but has not made clear just what should be done about the subspecific classification of the lizard.

Description.—Head somewhat narrowed and depressed; superciliary ridge slight; tympanum exposed; a well-marked fold of skin on each side of neck, making a characteristic groove; gular region without a fold; body moderately slender; tail tapering gradually to a point; head plates large and smooth; supraoculars bounded on each side by small scales; occipital plate large and very prominent; dorsal scales very strongly keeled and with strong posterior spines; scales of lower sides and abdomen smooth and without keels; femoral pores present; enlarged post-anal plates in males only.

Coloration varied; dorsal ground color light to dark brown; abdomen whitish; sides often brilliant blue; usually with two well defined stripes of clear yellow on each side; a series of dark brown lateral spots, which never connect to form undulating lines, usually present above and below the upper longitudinal stripes.

In order to study the variation in size and proportion of this lizard 108 Kansas specimens were measured. The data are as follows: Length of body, 21-62 (49-56); length of tail, 24-81 (61-70); total length, 45-140 (111-120); width of head, 5-12 (8-9); length of tail as percentage of total length, 48.3-61.1 (56-58); width of head as percentage of body length, 13.5-24.1 (16-18).

Ellis and Henderson (1913) gave the maximum total length as 203 mm., a figure decidedly above the maximum found in Kansas specimens. Taylor (unpublished) listed the following measurements: total length 160 mm., body length 68 mm., and tail length 92 mm. These figures were obtained from a much larger Kansas specimen than the writer has been able to examine.

Habitat and Habits.—Regarding the habitat of this subspecies, Cope (1880) wrote that, "It is found on the ground, but always takes refuge in the trees, running on and around limbs with great agility." Ruthven (1907), however, found it to be "Principally a ground form; in the mountains being found about rocks, and in the plains, about the foot of bushes." Strecker (1908) wrote that most of his specimens were collected on rail fences and around old logs in the woods. Van Denburgh (1922) stated that "This species is usually found on the ground and retreats to holes in the earth, banks, or spaces under or between stones, and occasionally it resorts to trees." Over (1923) found it living in the sandhills of Washington County, South Dakota. Taylor (unpublished) quoted farmers in western Kansas as saying that "Large numbers of these lizards are found in wheat fields, especially under grain shocks." Taylor also stated that he had collected as many as five specimens under one shock of wheat.

Yellow-banded swifts are usually abundant where they occur. Rock formations, especially of sandstone, often harbor them, though many have been taken from sandy regions where there are no rocks. During the month of May, a number of specimens were found about the "Twin Mounds" near Lindsborg, McPherson County. Some were taken from a sandy pathway exposed to the full glare of the sun, and others were re-

moved from the sides of large boulders, which they scaled with ease. A few of these swifts were taken from prairie grass near a rock ledge in Ellsworth County, and several persons have found the chalk beds of Trego and Gove counties to shelter many specimens. The sand dunes of Stafford County, though probably less favorable to this subspecies than to *Holbrookia maculata maculata*, have their quota of both species. All yellow-banded swifts taken there were removed from the surface of the ground, with the exception of five, which were captured upon the sides of a farm shed which was covered with sanded tar paper.

The yellow-banded swift feeds upon a large variety of small insects, particularly beetles, ants and grasshoppers.

Little attention has been given to the study of the life history of this lizard. Shufeldt (1885) found seven eggs in the uterus of one female. Strecker (1910) reported two females with eggs, one having six, the other eight. Taylor (unpublished) stated that "Females taken in July had not yet deposited their eggs. One very large specimen was found to contain fifteen." The writer has found seven Kansas females to contain lots of seven, seven, eight, nine, nine, and eleven eggs, respectively, giving an average of eight eggs per female. On June 12, 1926, a specimen laid six white eggs which measured six by ten millimeters in size.

Distribution in Kansas.—S. undulatus thayerii is generally distributed over central and western Kansas. Further collecting in the counties in that area will very probably add to the county distribution list indicated by the following map.

Sceloporus undulatus undulatus. (Latreille).

Pine Lizard, Fence Lizard, Tree Lizard, Black Lizard,

Brown Scorpion, Eastern Spiny Swift, Pine Tree Lizard, Alligator Lizard, Scaly Lizard.

Stellio undulatus.—Latreille, 1802, Hist. Nat. Rept. 2:40 (type locality, "Les grands bois de la Caroline").

Sceloporus undulatus.—Wiegmann, 1828, Isis, p. 369.

Sceloporus undulatus.—Stejneger and Barbour, 1923, Check List N. Amer. Amph. Rept., p. 59.

Sceloporus undulatus undulatus.—Cope, 1900, Ann. Rept. U. S. Nat. Mus. for 1898, p. 370.

Description.—Head large and somewhat depressed; body moderately stout; ear opening present; no gular

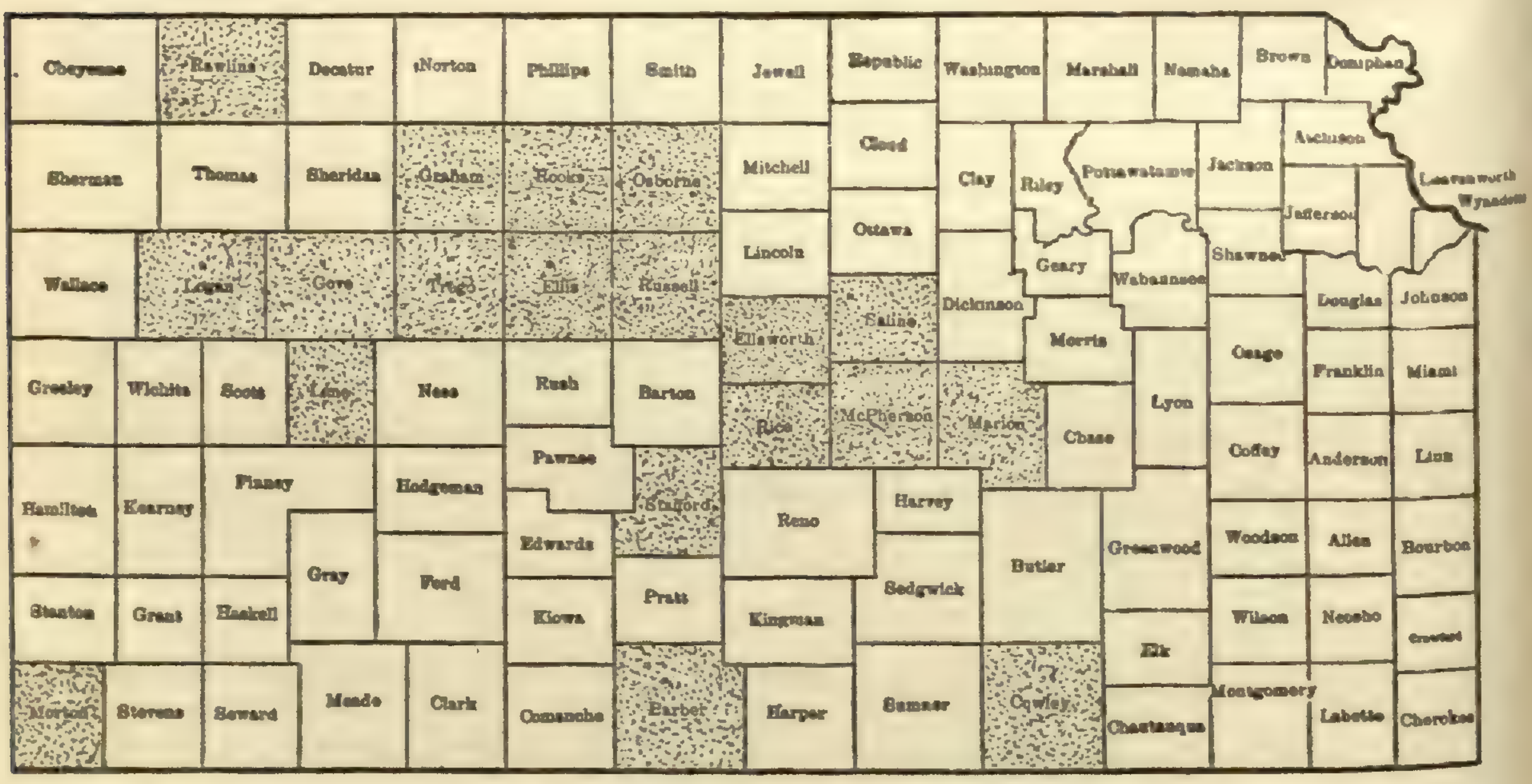

Fig. 3. Distribution of *S. undulatus thayerii* in Kansas as indicated by the county reports.

fold; neck groove conspicuous; tail moderately long; head plates large; occipital plate very conspicuous; supraoculars of medium size, bounded by a few small scales on each side; dorsal scales keeled and with strong posterior spines; abdominal and lateral scales smooth, with weak posterior spines; femoral pores present; enlarged post-anal plates in males only.

Dorsal color olivaceous or brown; sides often with at

least traces of two whitish or yellowish longitudinal stripes, which may be distinct enough in some specimens to intergrade with the condition usually found in *S. undulatus thayerii;* sides, also, with wavy, dark brown cross bars, approaching each other or overlapping on the back, and leaving not more than a narrow mid-dorsal band of solid ground color; ventral parts green, slate, olivaceous, or white; sides of abdomen and throat often blue; a diffuse streaking of blackish flecks present on the ventral surface.

The study of variation in the size and proportion of this species was made from 55 Kansas and Arkansas specimens. The data follow: Length of body, 34-67 (41-50); length of tail, 45-98 (51-60); total length, 80-162 (91-105); width of head, 7-14 (8-9); length of tail as percentage of total length, 49.5-61.4 (58-60); width of head as percentage of body length, 17.8-24.0 (18-20).

It is to be noted that the head widths of the two Kansas subspecies of *S. undulatus* have the same mode, and that the range of variation in most other proportions is nearly the same. Housholder (unpublished) attributed a wider head to *S. undulatus undulatus* than to *S. undulatus thayerii.* To test this distinction, twelve pairs of specimens, which measured the same in total length, were selected at random from the writer's data tables for each subspecies. The summary of the comparative head widths follows.

S. undulatus undulatus: Range, 8.0-10.5 mm. Average 9.017 mm.

S. undulatus thayerii: Range, 7.5-11.0 mm. Average 9.083 mm.

The difference in the head width of the two forms, as indicated by this comparison, is too small to be considered significant. However, the following summary,

which was obtained from the examination of the 55 specimens of *S. undulatus undulatus* and the 108 specimens of *S. undulatus thayerii,* does indicate a difference in the proportions of the two lizards.

	undulatus	*thayerii*
Mode of width of head as percentage of body length__	18- 20	16- 18
Mode of total length in mm.	91-105	111-120

It is apparent that the series of *S. undulatus undulatus* are on the average about 18 mm. shorter than the series of *S. undulatus thayerii,* and that the width of head as percentage of body length in the former lizard averages two millimeters greater than in the latter form. Hence, these data indicate a wider head in proportion to the body length for the subspecies *S. undulatus undulatus,* and conversely, a more slender body when compared with the width of head for the subspecies, *S. undulatus thayerii.*

So far as known, the measurements given by other writers for the pine lizard agree with those of the author.

Habitat and Habits.—Considerable mention has been given the pine lizard in the literature, because its widespread distribution has enabled many American naturalists to study it. De Kay (1842) stated that "It inhabits sandy and rocky situations." Holbrook (1842) wrote that "It is chiefly found in the pine forests of our country, being often under the bark of decaying trees. It chooses old fences as a basking place. It is exceedingly rapid in its motions, climbing with great facility to the tops of trees, and hence it is not taken alive without great difficulty." Smith (1882) wrote that "It prefers sandy and rocky soils, especially regions of pine forests, and apparently does not occur in wet places." Hay (1892) stated that "It is not disposed to seek safety by

flight, but by concealment. It will dive behind a trunk of a tree and while trying to dodge one hand may be caught by the other.'' Rhoads (1895) found it distributed all over the state of Tennessee below the elevation of 3,000 feet. Hay (1902) wrote that it was ''Very common in the higher and drier situations. It is often seen there during the warm days of summer, basking in the sunshine of some exposed rail fence or log.'' Hahn (1908) observed that ''They are very abundant in the woods and along fences.'' Allard (1909) stated that ''It is a very common lizard familiar to nearly everyone throughout the south. It is abundant in all wooded upland situations, and loves to bask in the hot sun, as it stretches out lazily at full length on a fence rail or rock. When disturbed it runs with great agility, usually up the nearest tree. On the tree trunk it usually moves so as to keep the tree between itself and the observer.'' Dunn (1915) stated that these lizards are found ''Chiefly on trees and fences, or very rarely on the ground. They are rather agile and difficult to capture, save with a noose. They do not, as a rule, go into holes when hard pressed, though I have seen one hide under the loose bark of a stump.'' Ditmars (1915) has found that ''Captive specimens require an abundance of sunlight and a perfectly dry cage.'' Wright and Funkhouser (1915), working in northern Georgia, found this lizard to be ''Abundant in higher and drier parts, and most common in the sandy pine lands where they seem to prefer the fallen timber, logs, and stumps.'' Deckert (1918) found the pine lizzard to be numerous on pine saplings and fallen timber in Florida. Barbour (1919) quoted Mr. A. G. Reynolds as writing that ''When on a burnt log *Sceloporus undulatus* often tries to escape capture by running a short distance then squatting suddenly to escape notice.'' Holt

(1919) published the record of a specimen feigning death for over twenty-five consecutive minutes. Blanchard (1922) found these creatures to be very common about rail fences, trees, fallen logs and stumps, and in fields or openings in woods. In escaping a pursuer they were seen in no case to run on the ground. The same author (1925) collected a specimen on an oak tree at Twin Caves, Indiana. Taylor (unpublished) stated that "They are often seen about roadsides in very dry or rocky places."

Several authors have given details which bear upon the life history of the pine lizard. Hay (1892) wrote that "The eggs are said to be laid in the sand, probably in little groups. They are deposited about June 1, and are hatched about July 10. The eggs are long and narrow and are covered with a tough coat, and are without any calcareous material. When laid they are abandoned to their fate, but the young are treated with the utmost tenderness by adults." Hay (1902) stated that "Eggs are laid early in the summer and hatch in July. By the latter part of August the young begin to shift for themselves and leave the company of the adults." Ditmars (1915) found that eggs may be hatched by placing them in moderately damp, not soggy, sphagnum moss, and keeping them at ordinary room temperature where their period of incubation is from six to eight weeks. Dunn (1915) stated that "A female caught on May 10, 1914, at Marlton, New Jersey, was killed and dissected on June 7. She had ten large eggs in her oviducts. My earliest record for young is July 29 (Nelson County, Virginia)." Hyde (1923) reported April 19, 1923, as a copulation date for the subspecies in Virginia. Speck (1924) recorded the attempted coition of a male of *S. undulatus undulatus* from New Jersey upon

a female of *S. spinosus* from Texas. Bishop (1926) found a large Kentucky female on June 24, 1925, with eight well-developed eggs in her body. Hassler (1927) reported the finding of five newly hatched young in New York in September, 1926. They were taken "among the leaves and grass at the base of a small ledge."

The above discussions indicate that from eight to ten eggs are laid sometime in June, and that they hatch a month or two later, depending upon the conditions of incubation.

The food of the pine lizard consists essentially of small insects and spiders.

Discussion of Kansas Records. — Because of the especial interest aroused by the question of possible intergradation in a place where the areas of distribution of two supposed subspecies approach each other, this heading is deemed a necessity. *Atchison County;* Prof. Felix Nolte of St. Benedict's College collected a pine lizard at Atchison in May, 1927. *Cherokee County;* Mr. W. H. Burt collected four lizards on September 6, 1926, near Shoal Creek, which Dr. Edward H. Taylor and the writer have identified as this subspecies. *Geary County;* Dr. F. W. Cragin (1881) gave a report from this area, and, unfortunately, his specimens have been lost. In addition to this, Cope (1900) reported four Townsend specimens from Ft. Riley under the United States National Museum number "4852." The data upon these specimens are obscure. This fact, the loss of Cragin's specimens and the knowledge that the distinctions upon which the two subspecies of *S. undulatus* are separated have often been close, is the basis of listing these as doubtful records. *McPherson and Rooks Counties;* These reports of Cragin (1881) are decidedly in the range of *S. undulatus thayerii,* and the specimens upon which they were based

have been lost. Therefore, the writer considers these reports as extremely doubtful ones. *Wyandotte County;* The work of Dr. Edward H. Taylor (unpublished) gave this report. Since Dr. Taylor has also collected this lizard in Swope Park, which is but a short distance from Wyandotte County, and Hurter (1911) listed it from a near Missouri County, this record is accepted as very probable.

Distribution in Kansas.—Kansas is on the very western edge of the distribution of this subspecies. Stejneger

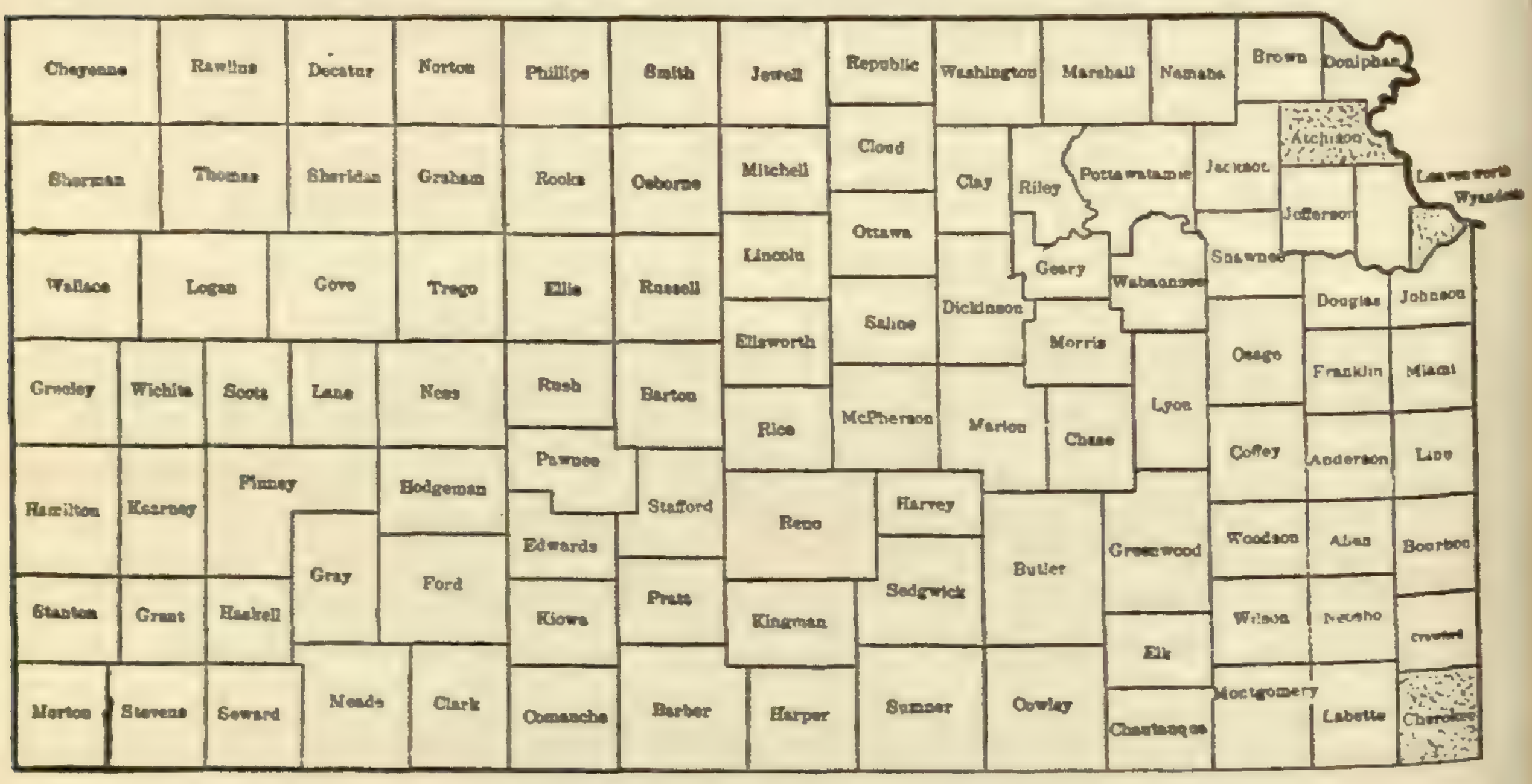

Fig. 4. Distribution of *S. undulatus undulatus* in Kansas as indicated by the county reports.

and Barbour (1923) gave the range as "Eastern States, New Jersey to Florida," but a review of the literature and the examination of certain specimens indicates that this does not adequately express the known range of the lizard. Specimens from Louisiana, Missouri, Arkansas and Kansas, examined by the writer are *S. undulatus undulatus,* and therefore, the range should very probably be "The Eastern States, New Jersey to Florida, westward to Louisiana and Eastern Kansas." Since a

specimen from Bloomington, Indiana, kindly sent to the writer by Mr. G. S. Myers, now at the Leland Stanford University, has been identified by Miss Doris M. Cochran of the United States Museum as this subspecies, and Blanchard (1925) reported it from Twin Caves, Indiana, the State of Indiana as a northern point in the known range is established.

The distribution of this subspecies in Kansas is probably confined to the eastern edge. A comparison of figures, 3 and 4, will show that in Kansas the distribution of *S. undulatus undulatus* is entirely distinct from that of *S. undulatus thayerii,* and that a space of several counties in which much collecting has been done, separates the known range of the two forms in the state.

Phrynosoma cornutum (Harlan).

Texas Horned Lizard, Common Horned Toad, Spiny Breasted Horned Lizard.

Description.—Head short; depressed; bearing prominent spines; two occipital spines, separated by a space in which there is a small, but easily discernable, median spine; two or three pairs of temporal spines of less prominence than occipitals; a short horn extending backward from the prominent superciliary ridge above each eye; muzzle descending steeply in profile; body dorsoventrally compressed; stout; bearing two rows of marginal abdominal spines; ear opening present, but often partly concealed by a fold of skin; both gular and neck fold present; upper series of labials smaller than lower series; sub-labials more prominent, increasing in size toward posterior end; tail short, broad and flattened at its root; dorsal scales small, excepting for sparsely distributed spines of varying prominence and sharpness; ventrals larger, weakly keeled or smooth; femoral pores few or absent in females, more in males; enlarged post-

anal plates not a reliable criterion of sex in this species; extremities well developed.

Coloration always dull; ventral parts white or ashy gray, usually with a smattering of blackish spots; dorsal color slate, brown, or blackish; vertebral stripe always pale or whitish, extending from occiput to base of tail; three pairs of dark spots along sides, these usually emarginated by pale whitish outlines; a dark spot on each side of neck; tail usually barred.

Measurements taken upon 96 Kansas specimens of this species are summarized as follows: length of body, 21-109 (51-60); length of tail, 7-44 (21-30); total length, 28-148 (76-90); width of head, 6-22 (12-14); length of tail as percentage of total length, 21.9-34.9 (28-30); width of head as percentage of body length, 13.5-37.5 (20-24).

In contrast to what has been shown in other species, this summary indicates that there is a greater variation in the length of body than in the length of tail, which is to be expected since the tail is relatively short in *P. cornutum*. The width of the head was measured just back of the angle of the jaw and did not include the temporal spines.

Hurter (1911) listed the total length as 110 mm., tail 46 mm., and body 64 mm., giving a tail percentage of 41.8, which is much larger than any noted on Kansas specimens by the writer. The measurements given by other workers for this species, so far as known, agree with those of the author.

Habitat and Habits.—There has not been a great deal written about the habitat and habits of this species. Winton (1914) and others have described the ejection of blood from the eye of certain specimens, but the writer has not been fortunate enough to observe this

phenomenon. Winton (1916) stated that "The favorite haunt seems to be along the edge of thick vegetation." He also gave evidence that the blood ejecting habit was connected with the process of molting. The same author (1917) wrote that "Male horned lizards sometimes fight each other in hot weather, if confined closely. . . . In North Central Texas, the horned lizards disappear with the first cold burst, which usually comes between the middle of September and the first of October," and (1916), "In the area of their greatest abundance they first appear from their winter burrows about the middle of April." Housholder (unpublished) stated that "Horned lizards are very common along roadsides within their range."

Horned lizards are strictly terrestrial in their habits, and are found most abundantly in dry, sandy areas where there is little vegetation. Hower, their distribution is not confined to sandy areas, for they often occur about limestone ledges. Individuals are frequently found close to dwellings, and may even breed in the dooryard. Horned lizards frequent the highways in some regions and pastures are often well populated with them.

The breeding habits of *P. cornutum* have been relatively well studied. Edwards (1896, 1903) has excellently described the nest digging habits. Strecker (1908) found "A set of eggs deposited in four layers of six each. . . The period of incubation is about forty days . . . the eggs are usually buried to a depth of six or seven inches and . . . the breeding season extends from the middle of April into the latter part of July." Givler (1922) has given a detailed account of part of the life history of the species as follows: "The lizards come forth about May 1. At first the males greatly pre-

dominate in numbers, but later the females come out of hibernation rapidly and tend to equalize the ratio. Matings take place freely in this early period and since the males are out of hibernation first, and in such numbers, the insemination of the females is insured. . . In May before ovulation there are usually about 32 eggs in the ovaries. . . It is evident that maturation occurs immediately preceding ovulation, and that fertilization occurs immediately after the entrance of the eggs into the ostium. The same female may copulate more than once, but ovulation of all the eggs takes place at nearly the same time. . . Eggs are laid under a ledge of rock in dirt and nicely concealed and covered from May until July. The incubation period is not known." Reese (1922) found that a female had laid three yellowish eggs on the night of June 7. Later, dissection showed 34 eggs inside of the body, similar to those laid before. Taylor (unpublished) stated that "The period of incubation is from four to five weeks." Cahn (1926) has called attention to the fact that a number of prominent zoologists have overlooked the knowledge of the egg-laying habits of certain species of the genus *Phrynosoma*. He has also given another interesting account of the nest digging habits of *P. cornutum*, stating that "On the afternoon of May 30, 1921, I chanced upon a female standing motionless on her toes in the center of a grassless, sunbaked area. The time was about 6:15 p. m. After about five minutes she began to dig. The work was leisurely done, but progressed steadily. . . . The lizard paid not the slightest attention to me, so early in the game I moved over and sat with her between my legs, the better to watch her operations. She permitted me to measure the hole, submitting to handling without objection, and resumed her digging opera-

tions immediately upon being released. By 8:30 it was too dark to see anything clearly, so I carefully marked her location and left her until morning. The lizard was gone next morning, and there was only the slightest trace to mark the spot where I had watched the performances of the previous evening. . . . Digging revealed the fact that the tunnel descended without turns to the depth of five and one-half inches. . . . This terminated in a circular chamber in which were laid 27 eggs, creamy white in color, and covered with a flexible leathery membrane.'' Eight of the eggs were left in Texas with a friend and hatched on the thirty-ninth day (July 8), while nine were removed to Wisconsin and hatched on the forty-sixth and forty-seventh days (July 15 and 16). Both sets were kept in the original sand, so the variation in hatching dates was attributed to temperature differences. Cahn also recorded the egg number in six sets which he had found, as follows: 27, 24, 25, 24, 23, and 25.

The natural food of the Texas horned lizard is chiefly ants and other small insects.

Discussion of Kansas Reports.—Horned lizards are presumably absent from Northeastern Kansas. Only two reports are available from this area for *P. cornutum. Douglas County;* Specimens have been taken at various times on or near the Kansas University campus, but none have been taken in other parts of the county. These lizards are admittedly the offspring of adults turned loose in the vicinity. *Franklin County;* Dr. F. W. Cragin (1881) reported this species from Ottawa on the authority of Prof. Wheeler. Though specimens have been collected in recent years at short distances to the south and west of Franklin County, none have been taken within its boundaries.

Distribution in Kansas.—The general distribution of *P. cornutum* covers the State of Kansas, with the exception of its northeastern corner.

Phrynosoma douglassii ornatissimum (Girard).

Ornate Horned Lizard, Girard's Short-horned Lizard, Ornamented Horned Lizard, Horned Toad.

Description.—Head depressed, with short spines; snout sloping gently forward, more abruptly as base is reached; tympanum exposed; occipital spine may or may not be more nearly vertical than last temporal spine when

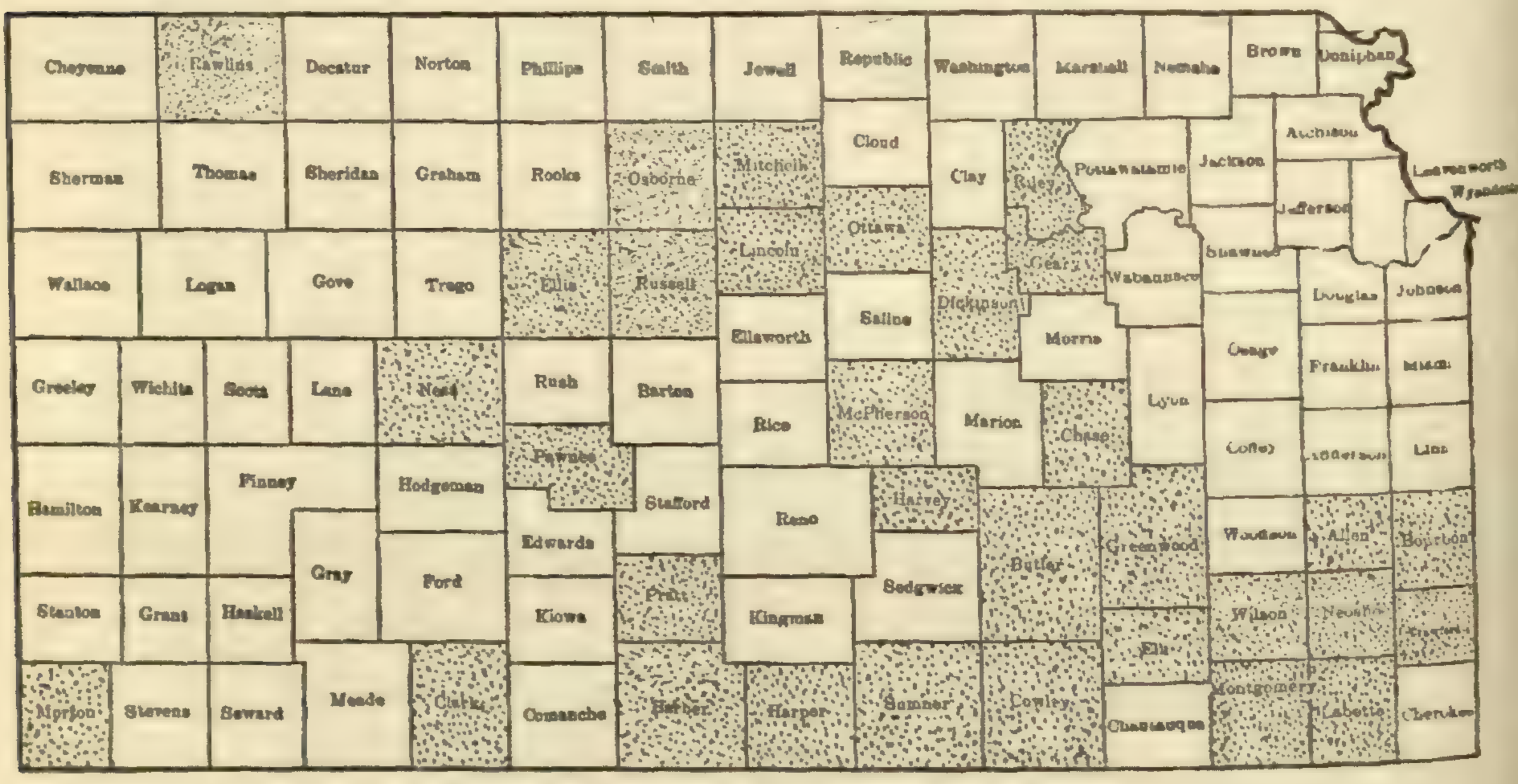

Fig. 5. Distribution of *P. cornutum* in Kansas as indicated by the county reports.

viewed from the side; spines set close together; median horn directed upward; four or five temporals, one occipital, and one prominent postorbital on each side; gular scales small and of nearly equal size; labials and sublabials pointing obliquely backward; dorsal scales of different sizes; few spines on back, central portion of considerable width practically free from spines; one row of marginal spines making a fringe on each side of the body; ventral scales smooth and small, arranged

in regular series, diagonally and transversely; both sexes with femoral pores; tail of female shorter than that of the male.

Coloration variable; dorsal color pale cinnamon rufous, yellowish, olivaceous, pinkish, brownish, or gray, and with uneven blotches of darker and lighter hues; tail colored like body; lower surface usually white or pale green, but sometimes greenish or olivaceous; head spines reddish to pale yellowish.

The study of variation has been made upon 36 Kansas specimens of this subspecies, twenty-two of which were small in size. A summary of the data is given below: Length of body, 20-91; length of tail, 9-40; total length, 31-131; width of head, 6-24; length of tail as percentage of total length, 24.3-37.1; width of head as percentage of body length, 21.4-30.0.

As far as observed, the measurements of other workers all fall within the ranges set by the above listing.

In addition to the two horned lizards discussed above *P. brevirostre* and *P. douglassii hernandesi* have been reported from Kansas, so it is necessary to consider them here.

The occurrence of *P. brevirostre* in Kansas has been regarded as very unlikely by Burt (1927).

Through the work of Cope (1900, pp. 414-415), *P. douglassii hernandesi* was definitely reported from Kansas. After carefully comparing specimens of *P. douglassii hernandesi* and *P. douglassii ornatissimum* from various points the writer has come to the conclusion that they may be synonyms and plans to make a careful study of their status later. The points upon which the two subspecies are presumably separated are *a more nearly vertical occipital spine*, as compared with

the temporal spine, in *P. douglassii ornatissimum*, and likewise a smaller opening between the occipital and temporal spines of *P. douglassii hernandesi*. Other variable characteristics have been used to discriminate between the two forms, such as coloration, number of spines on the body, and the occipital emargination. Cope (1900) attributed a deeper occipital emargination to *P. douglassii ornatissimum*, but found that the young present the form *characteristic* of *P. douglassii hernandesi*.

The occipital spines of Kansas specimens present great variation in their angle of rise from the horizontal plane. Some, with the occipital spines pointing backward, for example a specimen in the museum of the Kansas State Teachers' College at Hays, are probably *close* to *P. douglassii hernandesi*, while others with the occipital spine in a vertical position *are* no doubt *P. douglassii ornatissimum*. Moreover, there are intermediates between these extremes. Since no great differences are presented by the individuals in the series of Kansas specimens, it seems best to draw no complicated distinctions, and to consider them all as *P. douglassii ornatissimum*.

Habitat and Habits.—Little has been published about the habitat and habits of these lizards. They are insectivorous, and have been found to give birth to living young.

Discussion of Kansas Reports.—Since *P. douglassii ornatissimum* is evidently a rather rare Kansas lizard, a detailed discussion of its Kansas reports is given here. *Doniphan County;* Report given by Cragin (1881) as *P. douglassii*, and later by Housholder (unpublished) as *P. douglassii hernandesi*. Cragin's specimen has been lost, and consequently his data are obscure, and Hous-

holder's record is obviously based on Cragin's work. *Douglas County;* Report given by Taylor (unpublished) with the statement that "Some specimens have been turned loose about the University and are occasionally met with by collectors." *Edwards County;* This report is based upon a specimen in the Museum of Zoology of the University of Michigan. *Ellis County;* This report is based upon a specimen in the museum of the Kansas State Teachers' College of Hays. *Geary County;* The Hammond specimens reported by Cragin (1881) as *P.*

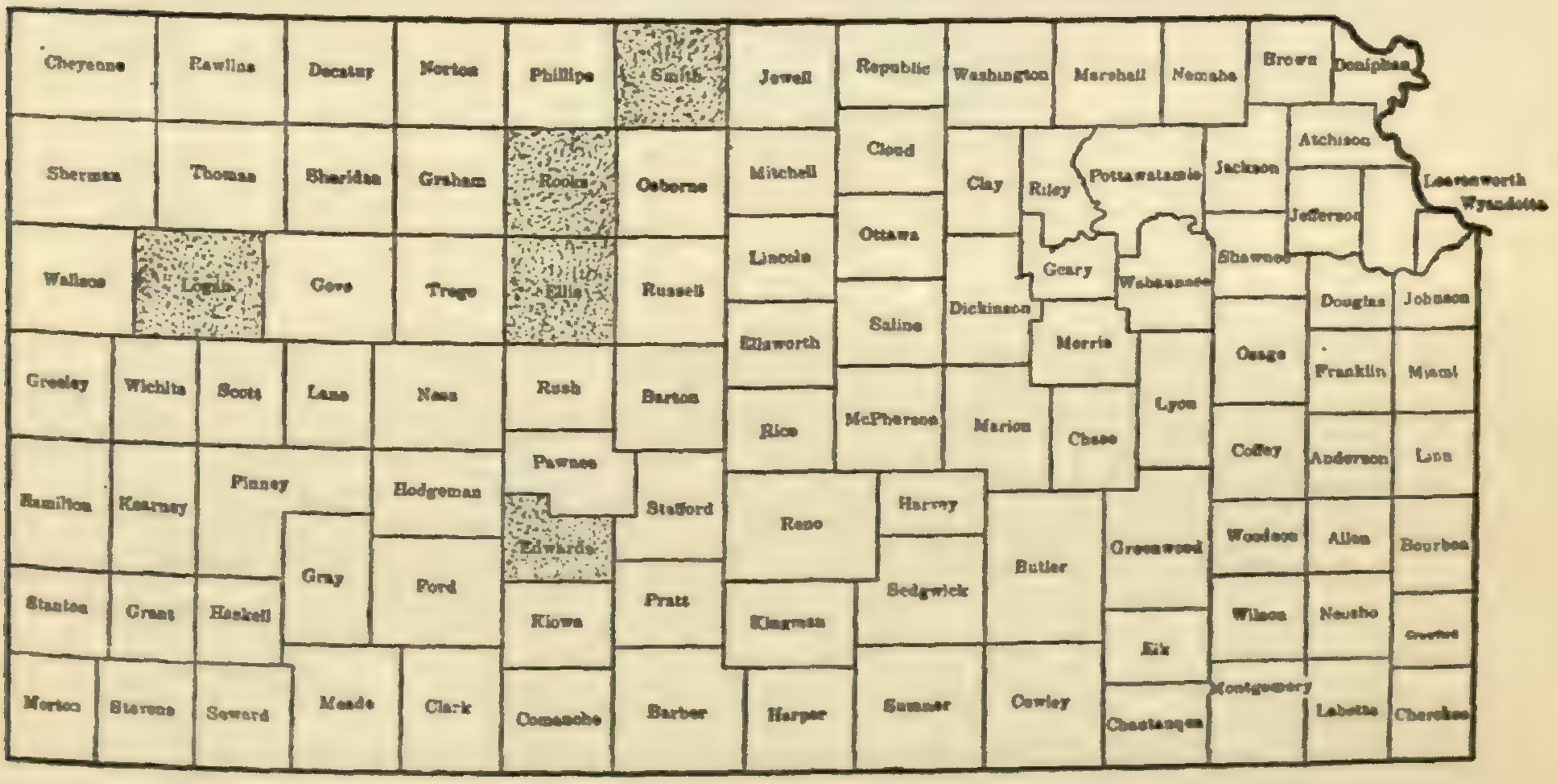

Fig. 6. Distribution of *P. douglassii ornatissimum* in Kansas as indicated by the county reports.

douglassii have been lost. Cope (1900) listed four specimens of the United States National Museum which were collected by H. Brandt as *P. hernandesi,* but the actual data of collection are obscure. *Logan County;* This report is based upon specimens in the Kansas University Museum. *Rooks County;* This report was given by Taylor (unpublished). *Smith County;* This report is based on a specimen in the Kansas University Museum. A number of specimens labeled "Kansas" are in the

museums of both the Kansas State Agricultural College and Kansas University.

Distribution in Kansas.—The distribution of this subspecies in Kansas is marked by several authentic records, all of which are in the western half of the state. Both *P. douglassii ornatissimum* and *P. douglassii hernandesi* are reported from Colorado, so the general range would probably include the entire western part of Kansas.

Ophisaurus ventralis (Linné).

Glass Snake,* Joint Snake, Hoop Snake, Grass Snake, Joint Lizard.

Description.—Head sloping gently forward, not well marked off from body; snout rounded; body serpentiform; tail long, usually incomplete, but tapering to a fine point in perfect specimens; the partly regenerated tail often a stub or spike; ear opening small; tympanum concealed; no gular fold; all scales smooth; body scales large, except in gular region; legs absent.

Color pattern varied; several dark longitudinal stripes on sides; mid-dorsal dark stripe present; wide light band on each side of median dorsal line; stripes not extending on head, but present on tail; ventral parts uniformly light colored; ground color for all upper parts, light to dark brown, never light grayish as in many eastern specimens.

As some of the common names imply, the tail is very brittle. The examination of 32 Kansas specimens of the species has shown only thirteen or 40.62 per cent with tails entire, giving a percentage of 59.38 for the nineteen deformed specimens. The largest amount of

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***This species is almost everywhere commonly designated as a snake because of its superficial resemblance to that group. However, the presence of ear openings and the absence of transverse ventrals shows its lacertilian affinity.**

regeneration, using as a basis of calculation the secondary length, was 32.35 per cent of that length.

Measurements taken on the 32 Kansas specimens of this lizard, mentioned above, are as follows: Length of body, 56-250 (201-250); length of tail, 248-438 (301-360); total length, 294-655 (501-600); width of head, 4.5-16 (10-12); length of tail as percentage of total length, 62.5-69.1 (68-69); width of head as percentage of body length, 3.0-7.0 (4.0-6.0).

The length attained by this species is in excess of tnat of all other Kansas lizards. Also, the width of head as percentage of body length is less than that of other species. Hay (1892) gave the total length of the largest specimen which he had measured as 915 mm., a figure greatly in excess of the largest one examined by the writer. Hurter (1911) found the total length to be 702 mm., tail 455 mm., and body 247 mm. Taylor (unpublished) measured a large Kansas specimen which has since been lost. His measurements were, total length, 700 mm., tail 456 mm., and body 244 mm.

Habitat and Habits.—This widely distributed lizard has often been collected. Holbrook (1842) stated that "This species chooses dry places for its abode, and passes much of its time in holes, or under the roots of old trees, and is often dug out of the earth with the sweet potato at harvest time." Hay (1892) wrote that "This animal selects for its abode, dry, rather than damp situations." Ditmars (1910), during several collecting trips in the south noted a condition pointing toward the noctural habits of the species. "There was a scarcity of specimens abroad during the day, but in the early morning, however, they were found in wells, where they had evidently tumbled during their nightly search for food." Taylor (unpublished) stated that "One speci-

men was found late in November buried eighteen inches under the ground about the foot of a hedge tree. It was coiled and motionless, but when brought out into the sun it showed signs of life.'' Evidently this individual had gone into hibernation.

The glass snake is frequently seen by farmers who are tilling the soil, or working in the hay or grain fields. It is a burowing form and is not often seen free above the surface of the ground. This accounts for its appearance in fields that are being plowed. Sometimes, however, the glass snake is found free above the ground, usually in the neighborhood of grasses or small grain patches. When disturbed it glides quickly away through the grass or weeds, a reaction which makes its capture difficult.

The glass snake feeds upon the larger insects, and very probably upon small rodents also.

Distribution in Kansas.—The distribution of the glass snake probably includes the eastern two-thirds of Kansas. This species is almost universally reported by the farmers of various state localities, but it is very hard for the collector to secure; therefore, its distribution in Kansas is probably much more extensive than has been shown, and further collecting is expected to add to these data. It is interesting to note that in spite of the tilling of the soil of their habitat some of these lizards are still able to withstand agricultural conditions, as indicated by their continued occurrence about cultivated areas.

Cnemidophorus sexlineatus (Linné).

Six-lined Race-runner, Six-lined Lizard, Six-lined Swift, Six-lined Whip-tailed Lizard, Race-horse, Sand-scraper, Race-nag.

Description.—Body slender; profile of snout blunter than that of either *C. gularis* or *C. tessellatus;* ear-open-

ing rounded anteriorly, somewhat flattened posteriorly; tympanum exposed; two prominent gular folds; head plates large; dorsals finely granular; large ventrals in eight longitudinal rows; dorsal caudal scales plated and strongly keeled; Gadow (1906) stated that the number of femoral pores varies from fourteen to nineteen, and a limited number of counts made on Kansas specimens by the writer are within these figures; these pores with enlarged centers in males; small centers in females.

Coloration extremely variable; ventral color purplish,

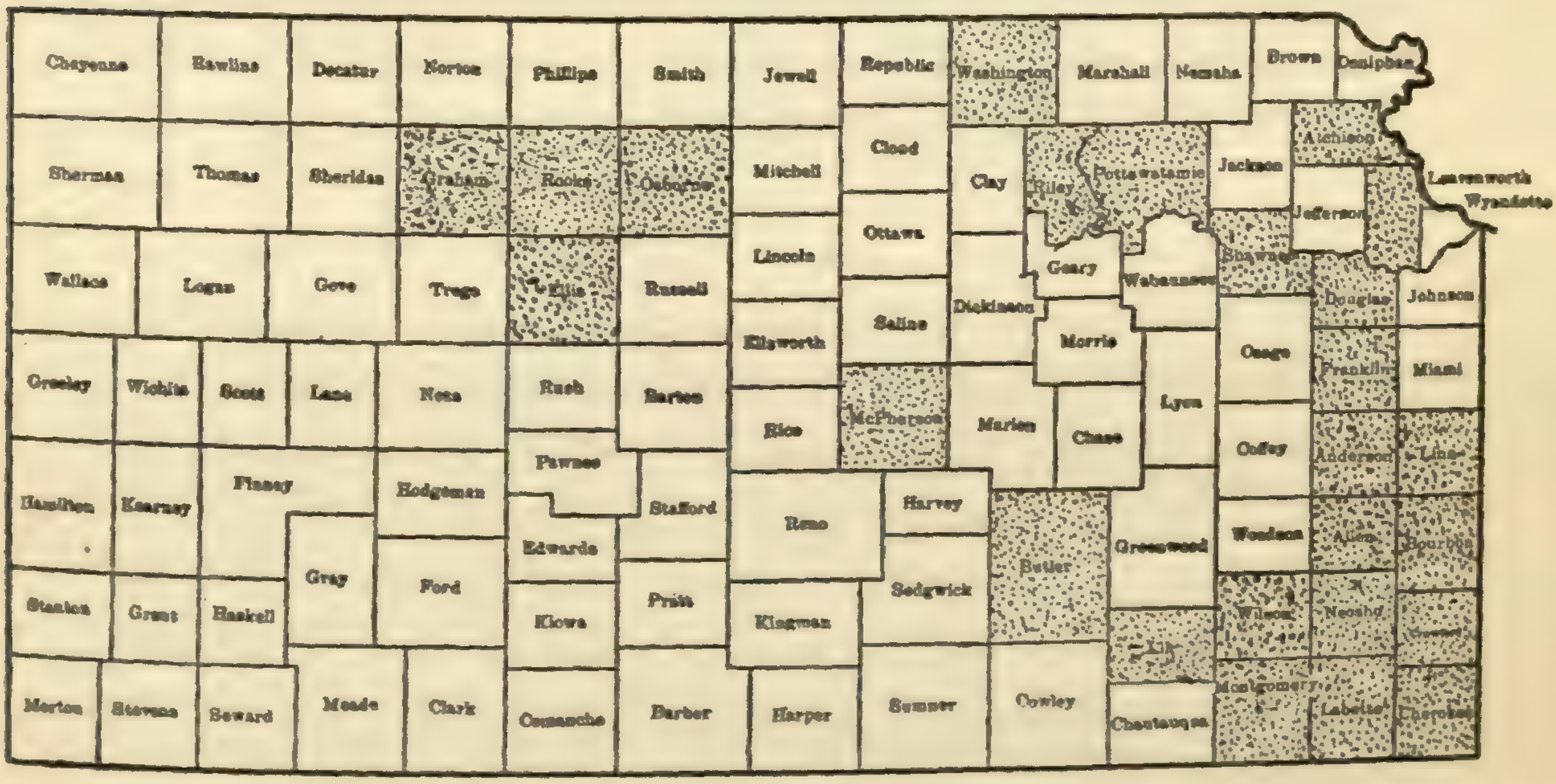

Fig. 7. Distribution of *O. ventralis* in Kansas as indicated by the county reports.

blue, greenish blue, bright green, yellowish, pure white, or brownish; sides dull bluish, whitish, yellowish, greenish, slate or purple; sides always darker than below, and often one of the above colors is found on the sides while the abdomen is gray or whitish; back with six longitudinal light lines; young specimens often with a broad seventh stripe down the median part of the back, which fades and gradually disappears as the animal becomes older; dorsal ground color usually some shade

of brown, gray, green, or yellow; upper head scales olivaceous; lower labials white, or light blue; upper labials brown, yellowish, or greenish; angle of jaw colored more deeply than labials; tail brownish above, whitish beneath. The coloration of these lizards should always be studied on freshly collected material or living specimens, for their colors fade very rapidly in preservatives.

Data upon 169 Kansas specimens are as follows: Length of body, 27-79 (61-70); length of tail, 45-164 (121-135); total length, 72-238 (181-200); width of head, 4.5-11 (8-9); length of tail as percentage of total length, 55.5-72.1 (66.1-68); width of head as percentage of body length, 11.1-17.7 (12-14).

This summary indicates a greater variation in the length of tail than in the length of body. Pratt (1923) gave the total length as 250 mm., and tail 175 mm. This figure for total length is the greatest yet found by the writer.

In discussing the genus *Cnemidophorus* it is well to note that besides *C. sexlineatus,* the species, *C. tessellatus* and *C. gularis,* have been reported from Kansas. The writer has examined over 200 specimens of racerunners from Kansas, and has referred them all to *C. sexlineatus.* The report of *C. gularis* for Kansas was made earlier than that of *C. tessellatus* and will be considered first.

Hallowell (1856 a-b) reported one and seven specimens of *C. gularis,* respectively, from Kansas. They were presented to the Academy of Natural Sciences of Philadelphia by Dr. Hammond, U. S. A., who was stationed at Ft. Riley, Kansas. The recent trip of the Kansas University Biological Survey through that region (1926) has failed to reveal any of these specimens, and

the range of *C. gularis*, as given by Stejneger and Barbour (1923), does not include Kansas. After considering the obscurity of the report (1856) and the corresponding possibility of error in recording the exact locality of the specimens, *C. gularis* is withheld from the Kansas faunal list.

Cragin (1884) reported *C. tessellatus* from Central Kansas, writing that "The occurrence of this species in Kansas was hardly expected, but a specimen of the typical variety has been sent to me from McPherson County by Dr. John Rundstrom." Thus it is clear that the report of this lizard for Kansas is based upon a single specimen, which has since been lost. The writer has collected and examined eight race-runners from the same locality (near Lindsborg) in which Rundstrom worked, and they are all *C. sexlineatus*. The range of *C. tessellatus*, as given by Stejneger and Barbour (1923), is "Texas to California, also Utah, Colorado and Nevada." Van Denburgh (1922) listed it as a Kansas species, but Cragin's work was cited in his bibliographic references, thus making evident the basis of his report. In view of the existing data it seems best to regard *C. tessellatus* as a species unlikely to occur in Kansas, and to withhold it from the Kansas faunal list.

Habitat and Habits.—C. sexlineatus is probably the most widely distributed lizard in the United States. Its range, according to Stejneger and Barbour (1923), is "Maryland to Florida, west to Northern Mexico and Arizona and up the Mississippi Valley as far north as Lake Michigan." A lizard which occurs over such an area is certainly able to adapt itself to a large number of habitats, and consequently its habitat and habits have been discussed by a large number of herpetologists.

Cope (1866) wrote that "They live chiefly in dry, open woods, among dry leaves, at the foot of bushes, etc. They are emphatically ground lizards, and not a tree or rock species." The writer takes exception to the statement that this lizard is not a rock species, since he has found it under rocks in many localities. However, it is not always a rock species as will be shown by further discussion. Cope (1880) wrote that "It is entirely terrestrial in its habits and moves with greater rapidity than any other lizard." Rhoads (1895) found that "This lizard was numerous in the suburbs of Chattanooga along railroad embankments." Ruthven (1907) specified that "This is a characteristic form of the desert floor habitat." Ditmars (1915) stated that "They frequent dry, sandy places and borders of dusty roads. . . . When disturbed they dart into their holes or burrows with lightning like rapidity." Wright and Funkhouser (1915) wrote that "It is found in plowed ground and cornfields, and seems to prefer the bare furrows for sunning. . . . They dart into holes in the raised earth between the furrows when disturbed. The burrows extend in an irregular direction to a depth of eight or ten inches." Holt (1919) found that a young specimen was very restless, and the moment it was released, it darted away with the speed characteristic of the species." Blanchard (1922) wrote of specimens of western Tennessee, "They are extremely common in sandy situations near Henry and are always found on the ground. They are swift and escape by running into grass or brush. Overnight, some at least, remain in holes dug in the sand, from which they may easily be taken early in the morning. The burrow is short and has two openings, and when the lizard is inside one of these openings is partially filled with sand thrown out from within." Hallinan (1923) observed

these race-runners going in and out of gopher tortoise burrows in Florida. Dr. Edward H. Taylor of Kansas University in a recent interview stated that while he was collecting in Tennessee during the summer of 1926 he found *C. sexlineatus* occuring abundantly in a heavily forested region on a bank of the Tennessee River, over which rose a hill that was covered with limestone ledges.

The writer has often collected this lizard. It frequents a greater variety of habitats than all other Kansas species, and it seems that only a high moisture content of the surface soil restricts its distribution, since it has often been collected from rocky ledges and sandy areas, but only rarely from loamy situations. It has been found on rocky hillsides, open corn and wheat fields, upland meadows, low sandy river banks, about chalk cliffs, railroad embankments, road beds, sand dunes, isolated sand banks, occasional out-croppings of rock, and on the upper part of wooded hillsides. These creatures are often found close to dwellings, and are apparently able to adapt themselves to changes brought about by agricultural conditions.

These race-runners are probably the swiftest of Kansas lizards. Taylor (unpublished) found them to be very common in the chalk cliffs of Trego and Gove counties, but obtained only a small number because of their great agility. No doubt the swiftness of this lizard in escaping its numerous enemies, including man, is responsible in a large measure for its ability to survive even in the more populated districts.

In regions where there are no rocks for hiding, members of this species dig holes in which they stay at night. These holes are probably used repeatedly, and often when a specimen is disturbed in the day time it runs rapidly away, and finally disappears into one of them.

In Wilson County, near the towns of Neodesha and New Albany, many burrows were observed in the graveled right of way of the Frisco railroad. These lizards are very graceful and their running movement is even. Specimens running at top speed always went in a straight line, all four legs being employed in perfect unison. A distinct elevation of the body is accomplished by the straightening of the legs, so that the body is carried parallel to and distinctly above the ground.

The writer has carried a small revolver with him while collecting, and has obtained large numbers of specimens with shot shells. Many of these could not otherwise have been taken. In order to get the most specimens in the least time the habits of these creatures were studied, and often peculiarities in their behavior were used to maneuver them into the open. Short, swift runs are often made by *C. sexlineatus* when it is disturbed. These are followed by pauses during which it holds its head high in the air in a manner indicating keen alertness and watchfulness. If the disturber moves away, the lizard usually remains motionless, but if he comes closer, the animal soon darts to another position. Usually movements to the side do not cause the lizard to run. Always the movement of the observer must correspond to the rest periods of the lizard. The movement of the lizard is betrayed by a faint rustle which is readily perceived by the collector.

The six-lined race-runner is perhaps the most gregarious of all our lizards. Specimens were nearly always found at certain points, even though the collector returned again and again, whereas, at points not far away, which looked equally attractive as a habitat, no specimens were seen. Thus, localization of the habitat in definite areas seems to be characteristic of the species. At

Lawrence this lizard was collected along the Union Pacific railroad track amid coarse rock and considerable vegetation very close to the Kansas River. A specimen was driven into a rock cliff in Washington County and was dug out only after the removal of a considerable amount of rock. It had followed a small tunnel for a distance of almost five feet.

The breeding habits offer a good field for further study. Ditmars (1915) stated that "This species lays thin-shelled eggs. The female scrapes out a small hollow in the sand, and carefully covers the eggs, leaving them to be hatched by the sun's heat." Wright and Funkhouser (1915), working in Florida, found that "The eggs were deposited in irregular burrows between furrows in a plowed field. These burrows were eight to ten inches deep. The eggs, measuring about sixteen by ten millimeters in size, and deposited in sets of four or five, are laid in June."

Six-lined race-runners are very fond of spiders and many small insects, especially grasshoppers and Lepidoptera. A number of snails have, also, been found in stomachs examined.

Distribution in Kansas. The six-lined lizard appears to be distributed throughout the state and has been reported from all adjoining states. It has already been mentioned that *C. sexlineatus*, *Sceloporus undulatus thayerii*, and *Holbrookia maculata maculata* are the only species taken in certain parts of western and central Kansas. In the isolated outcroppings of rocks which are found in Washington and Republic counties, this lizard and *Eumeces obsoletus* are the only species reported, and they have frequently been found together.

Leiolopisma laterale (Say).

Ground Lizard, Brown Backed Lizard.

Scincus lateralis Say, 1823, Long's Exp. Rocky Mts. 2:324, (type locality, "Banks of the Mississippi River below Cape Girardeau, Missouri").

Scincus unicolor Harlan, 1825, Jour. Acad. Nat. Sci. Philadelphia, 5:156.

Lygosoma laterale Cragin, 1881, Trans. Kansas Acad. Sci., 7:118.

Leiolopisma laterale Jordan, 1899, Man. Vert, Northern U. S., ed. 8. p. 201.

Description.—Body elongated, cylindrical; limbs min-

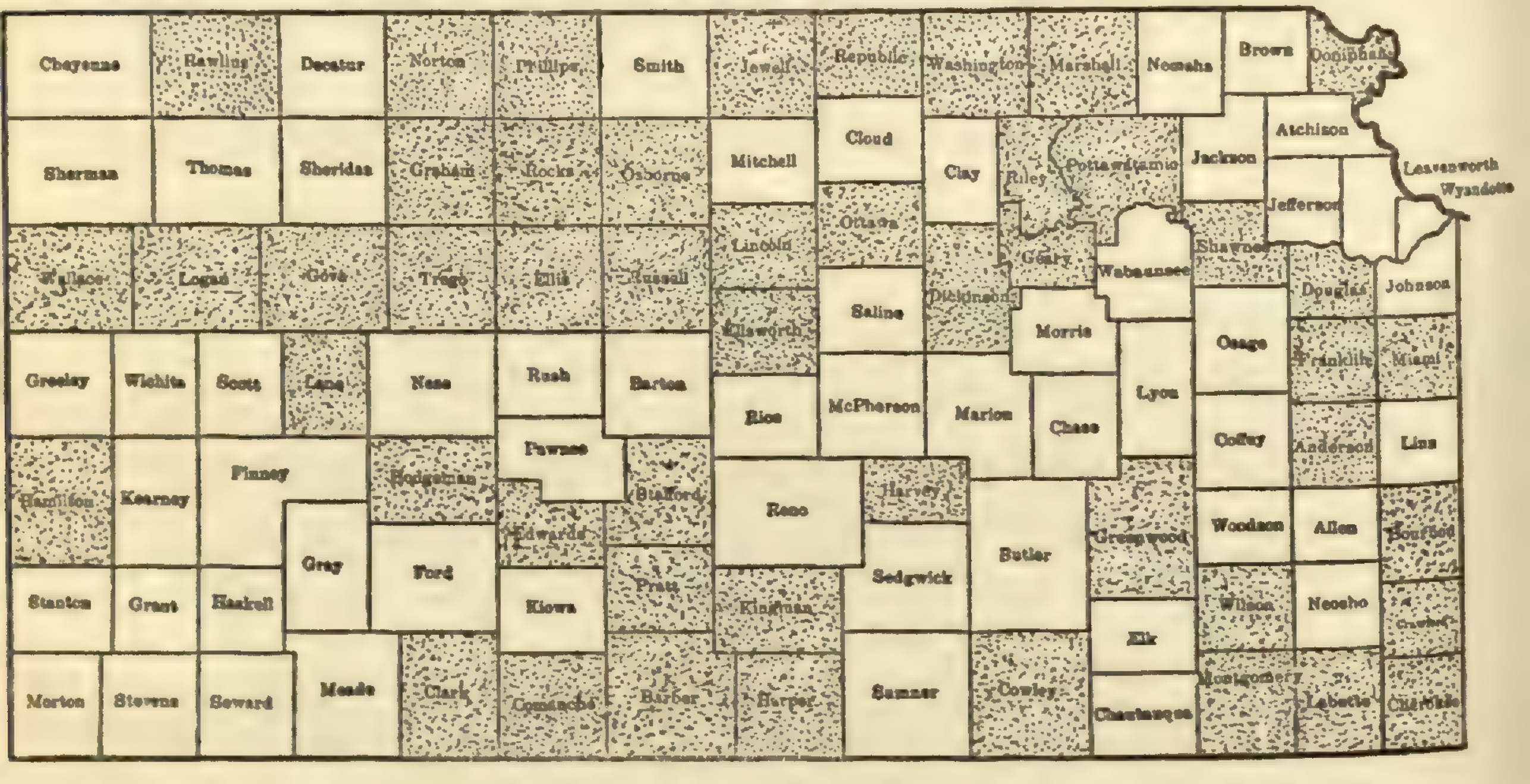

Fig. 8. Distribution of *C. sexlineatus* in Kansas as indicated by the county reports.

ute; ear-opening present; scales small and arranged in longitudinal rows.

Coloration with little variation; body with a broad, dark brown band on each lateral surface; also, a broad dorsal band of bronze or light brown; back often with minute flecks of dark brown which are arranged in a more or less regular row on each side of the vertebral line; lateral stripes extending on head and tail; ventral parts white, silvery, or yellowish in color.

Data taken upon 48 Kansas and Arkansas specimens of this species are as follows: Length of body, 19-81 (41-50); length of tail, 23-84 (61-70); total length, 49-136 (91-120); width of head, 3-6 (4-5); length of tail as percentage of total length, 45.5-75.5 (60-65); width of head as percentage of body length, 7.4-15.8 (10-12).

Since the tail of these lizards is very brittle and breaks easily many specimens are found with short or incompletely regenerated tails. All measurements given in the literature for this species, so far as known, fall within the ranges given in the above listing.

Habitat and Habits.—The ground lizard is found to range over a large part of the eastern and southern United States, and Kansas is on the extreme western border of its range. Holbrook (1842) stated that "This species may be found by the thousands in the thick forests of hickory and oak in the Carolinas and Georgia. . . . They emerge from their retreats after sunset, in search of small insects and worms on which they live. They take shelter quickly when disturbed, and do not climb." Hay (1902) found this lizard to occur "Most often under logs in rather damp situations." Ditmars (1915) wrote that "It is very secretive in its habits and leads a burrowing life. Large numbers of specimens are found under the loose bark of fallen trees." Wright and Funkhouser (1915) gave the distribution of some specimens taken in Georgia as follows: "One was found under the bark of a log at the edge of a small stream. The log was almost in the water. One was found under leaves in the woods, and the rest on the ground in open spaces." Deckert (1918) stated that this lizard is "Common under bark in damp situations."

Ground lizards taken in Kansas have always been found in woods or very near to them. Some live among the rocks on wooded hillsides, usually near a stream, but more inhabit the damper, heavier woods. There appears to be little doubt that a humid character of the surface soil favors the occurence of this species, and conversely, that a lack of moisture in the surface soil restricts its distribution. The writer has often taken specimens by turning over hillside rocks in the spring. In the summer the ground lizard is seldom found under rocks, but occurs then under the dead leaves and grasses of the woodlands, where its presence is often betrayed by a slight rustle. Attempts to capture these creatures often result in failure because of their wonderful agility and the extreme brittleness of their tails. In a few instances the writer has been able to secure a specimen by grasping a handful of leaves in which the lizard had concealed itself.

Very little has been recorded about the breeding habits of this diminutive lizard. Strecker (1908) found that "The eggs of *L. laterale* are three or four in number, and are deposited under the bark of fallen trees, or in hollow logs. They measure about nine or ten millimeters in length." The dissection of a specimen from Douglas County, Kansas, revealed the presence of six eggs in the oviducts.

Distribution in Kansas.—As indicated by the map, *L. laterale* is generally distributed over the eastern third of Kansas. This area, characterized by streams with wooded banks, receives the greatest amount of the rainfall of Kansas as indicated by the report of the Weather Bureau, United States Department of Agriculture (1923). Dry and sandy areas do not yield this species,

and, therefore, it will probably not be taken in western Kansas.

Eumeces anthracinus (Baird)

Coal Skink, Black Skink, Anthracite Skink.

Description.—Ear opening present; all body scales in longitudinal rows; legs only moderately stout; *cheeks never buldging;* toes elongated; nails short. (A co-type in the United States National Museum has short toes and

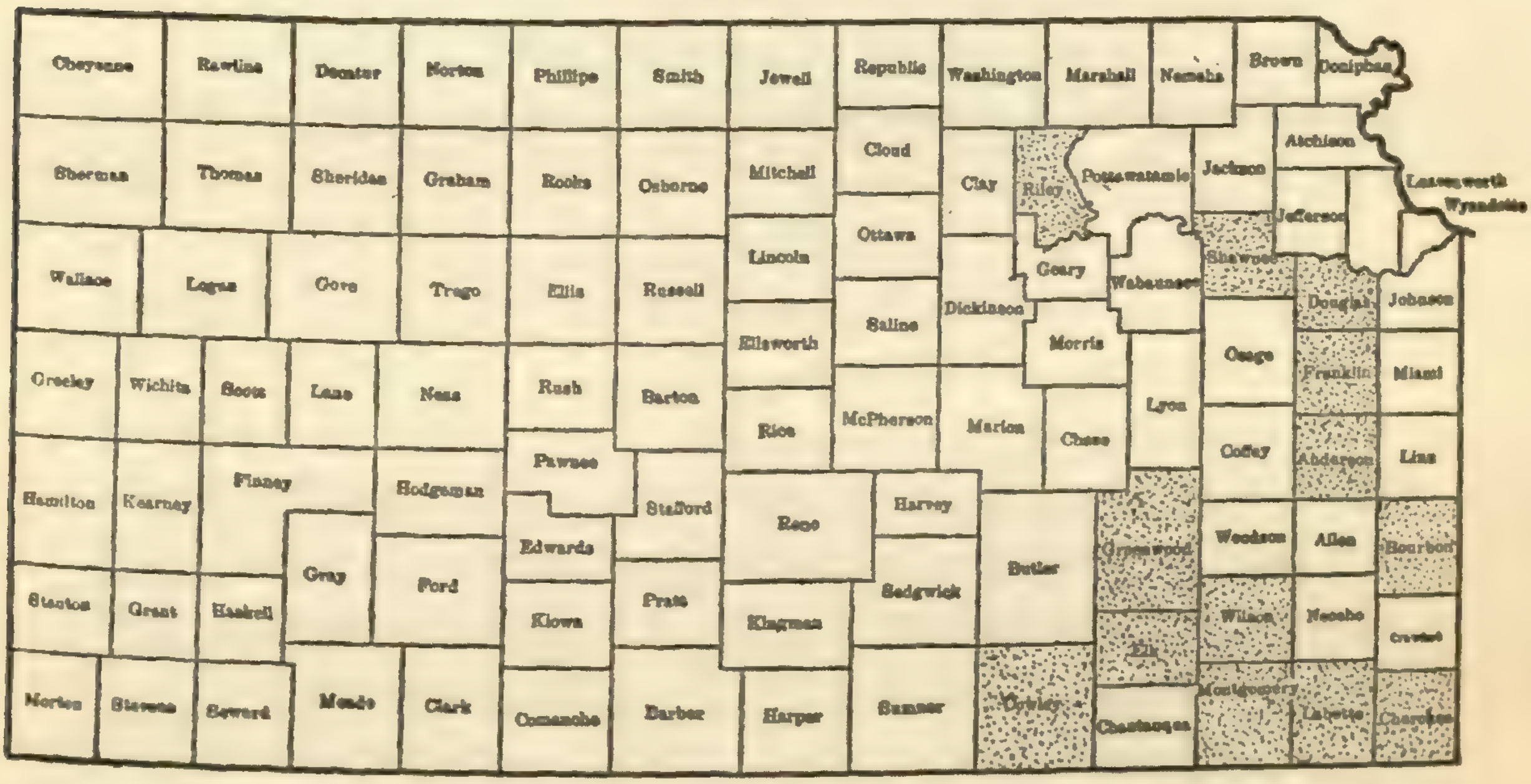

Fig. 9. Distribution of *L. laterale* in Kansas as indicated by the county reports.

heavy, thick limbs, according to information kindly furnished by Dr. L. Stejneger.)

Coloration varies somewhat with age; *young,* usually with an almost uniform blackish color; however, as a result of differential coloration, a broad, jet black band may be seen on each side, but it sometimes requires a careful examination to do this; *adults,* usually lighter in color; ventral parts bluish or yellowish; upper surface uniform blackish or olivaceous; all specimens with an intense, dark, broad band on each side, bordered above and below by narrow light lines; the wide dorsal

band *uniform* in color, darker than upper bordering stripes, lighter than lateral bands.

Seventeen Kansas specimens of this species have been measured, and the data are as follows: Length of body, 23-61; length of tail, 38-96; total length, 70-146; width of head, 4-9; length of tail as percentage of total length, 47.0-65.8; width of head as percentage of body length, 13.1-16.0.

A longer specimen than any designated in the above summary was examined by Hurter (1911), who gave the total length of the coal skink as 157 mm., tail 101 mm., and body 56 mm.

A Kansas lizard, collected by Mr. Jack Sterling at Carlton, Dickinson County, Kansas, has been recently identified by the United States National Museum as *E. pluvialis*. Dr. L. Stejneger and Miss Doris M. Cochran have compared this specimen with the co-type of *E. anthracinus* and find that the former has long toes, and delicate, slender limbs, in contrast to the short toes, and heavy, thick limbs of the co-type of *E. anthracinus*.

A detailed study of the variation presented by specimens of *E. anthracinus** from various points throughout its range, and also related work with other species of lizards, has clearly indicated to the writer that the length of both the legs and toes is a highly variable characteristic, which, though of considerable importance in determining affinities, is usually not of primary significance in the identification of closely related species. Therefore, it appears that *E. pluvialis* may be a synonym of *E. anthracinus*, and consequently, all Kansas specimens of this section of *Eumeces* will be discussed here under the head of *E. anthracinus*.

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*The writer intends to present these data, and also a discussion of the relationship between *E. anthracinus* and *E. pluvialis* in a forthcoming paper.

Habitat and Habits.—The coal skink is a rare lizard and records of its habitat and habits have not been found by the writer in the literature. This species occurs in Franklin County in considerable abundance, and according to Mr. Howard K. Gloyd, now of the Kansas State Agricultural College, it is found under hillside rocks, as are many other species of *Eumeces.* It feeds upon a variety of small insects and, so far as known, is entirely insectivorous.

Discussion of Kansas Reports.—Since this is the first work to report the occurence of this species in Kansas, all available state records are here given in detail. *Anderson County;* Report based on a specimen in the Kansas University Museum. *Dickinson County;* This report is based on a specimen in the Kansas University Museum which has been referred to *E. pluvialis* by Dr. L. Stejneger; the record of this specimen (No. 744) is under the name of *E. anthracinus. Franklin County;* A fine series of these skinks, most of them collected by Mr. and Mrs. Howard K. Gloyd, are in the museum of Ottawa University. *Miami County;* This report is based on a specimen (No. 201) in the museum of Ottawa University.

Distribution in Kansas.—The coal skink is evidently confined to the eastern half of Kansas in its distribution, and its known range is within that of *E. fasciatus.*

Eumeces fasciatus (Linné).

Five-lined Skink, Blue-tailed skink, Scorpion, Striped Lizard, Red Headed Lizard.

Description.—Body elongated, sub-cylindrical; head widest anterior to the ear opening; all scale rows longitudinal; sides of head generally bulged in adult males, usually not in females; either one or two transverse mentals present under chin.

Coloration varies greatly as these lizard develop; em-

bryos with five whitish longitudinal lines on body at least two weeks before time of hatching; newly hatched *young* with brilliant blue or purplish blue tails; body dark in color; all lines distinct; median line bifurcating on head; as young develop the dorsal surface becomes grayish, and undergoes a *differential coloration*, each scale having a perceptibility lighter area in its center which is continuous with a lighter emargination of the posterior border, the anterior and lateral borders

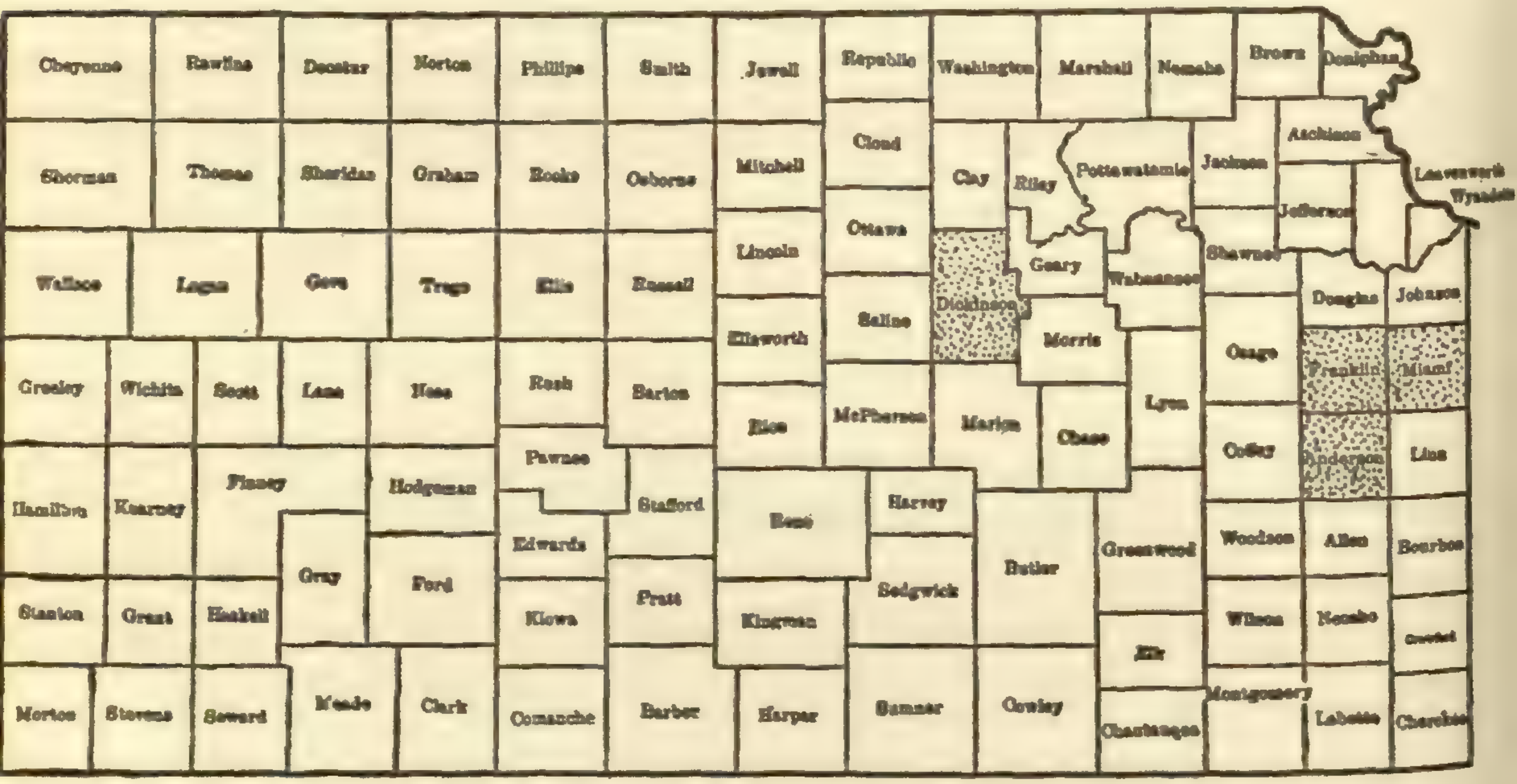

Fig. 10. Distribution of *E. anthracinus* in Kansas as indicated by the county reports.

darker; sides remaining dark between and below the two lateral stripes; *adults* becoming lighter above and then later laterally; all stripes tend to become obsolete with age in both sexes, the center stripe disappearing before the lateral stripes; cheeks of adults red, or brownish red, in color; all stages white under head, and also in gular region; under surface of legs often light; other ventral parts dark, usually slate colored.

Data upon 93 Kansas specimens of this species follow: Length of body, 22-90 (61-70); length of tail, 22-

119 (81-90); total length, 50-189 (136-150); width of head, 4-15 (8-10); length of tail as percentage of total length, 44.0-65.2 (60-65); width of head as percentage of body length, 11.8-20.8 (14-16).

All works that the writer has consulted give larger maximum measurements than those of the above summary. Harlan (1829) gave, under the synonymous name, *Scincus erythrocephalus,* the measurements of what was probably a large adult male, as total length 254 mm., tail 165 mm., and body 89 mm.

Habitat and Habits.—The western edge of the distribution of this species passes through Kansas. The five-lined skink is common in many parts of the southern and eastern United States, as well as at some central and northern points. Holbrook (1842) wrote that "The young live mostly on the ground, but the adults ascend trees and are seldom seen on the ground. . . . Sometimes adults utilize old woodpecker holes for their abode." Smith (1882) found these specimens "Under bark in May." Rhoads (1895), working in Tennessee, found the five-lined skink in the western lowlands only. Hay (1902) stated that "They are very shy and timid, and spend much of their time hidden under leaves and bark or in trees." Allard (1909) wrote of Georgia specimens as follows: "They are very common. In every field and wood they may be found basking in the sun or running with great rapidity over the ground. They are frequently found under the bark of fallen trees, and decayed stumps." Wright and Funkhauser (1915) also wrote of Georgia specimens "They are often found in deserted buildings, in chimneys, and also on fences, but seldom seen on the ground or on trees." Deckert (1918) stated that this lizard "Inhabits hollow trees, always near water." Blanchard (1925) found "Two small speci-

mens, which were taken from under the bark of a log over a small stream in heavy woods in Vanderburgh County, Indiana." Taylor (unpublished) stated that "They are usually found under stones around limestone cliffs." Bishop (1926) found a Kentucky specimen under a railroad tie.

The five-lined skink has been taken in a variety of Kansas habitats, but nearly always in wooded situations very similar to those occupied by the ground lizard, *Leiolopisma laterale*. A humid character of the surface soil is probably more favorable to this species than to any other North American member of the genus *Eumeces*, and heavy woods, especially those with rocks and underbrush which are near a stream, are typical of the Kansas habitat of *E. fasciatus*. North of Neodesha, Wilson County, on July 27, 1926, three recently hatched blue-tailed young were taken along the edge of the Verdigris River among large fallen rocks from a ledge which rose 30 to 40 feet above. A spot near the town of Fall River, Greenwood County, where rocks tower 20 to 40 feet above the Frisco right of way, also yielded three young specimens on the following day. The bed of the Fall River was on the opposite side of the railroad track, and the humid nature of the habitat was clearly indicated by a growth of mosses and ferns at the base of the rocky ledge. After a climb to the top of the ledge no more specimens of *E. fasciatus* were observed, but a specimen of *C. sexlineatus* was taken.

Northwest of New Albany (Elk County) an adult specimen was observed in a tree about fifteen feet from the ground. Another specimen was found at sunset playing on an old dead log in a cemetery. While collecting at Lawrence, Douglas County, a medium-sized specimen was observed to run into a hollow stump about three

feet high. The holes at the bottom and at the top of the stump were both closed. Then a sack was placed over the bottom hole which was opened while the top one was left closed. The lizard would not, however, go into the trap prepared for it as a snake would probably have done. The principle was reversed, the bottom hole being plugged and the top one opened and covered with the sack, whereupon the skink ran upward and was captured.

Several writers have written notes bearing upon the breeding habits of *E. fasciatus*. Smith (1882) found that "It lays nine oval eggs at a time." The egg sets found by Strecker (1908) were all of eight eggs each. Allard (1909) reported the finding of seven eggs in a cavity under the bark of a rotten log. A total of twelve eggs were recorded for a female by Dunn (1920). After collecting in western Tennessee, Blanchard (1922) wrote that "An adult female with nine eggs was found on July 12, under the loose bark of a fallen tree in the woods. The eggs appeared to be in no special cavity, but merely lay in the damp rotted wood, between the bark and the harder wood beneath." Lindsdale (1927) reported seeing young in Doniphan County, Kansas, as early as June 12, 1923, but the writer is inclined to believe that they were some that had hatched during the previous season.

A female collected at Lawrence, Douglas County, by Mr. W. H. Burt on May 17, 1926, laid a set of six eggs on June 12. Another female with eleven eggs was taken in the same locality on June 18. Both the skink and the eggs were found in an old rotted log which occupied a shaded position near a creek bed. Young of this species were found by the Kansas University Biological Survey about July 26, 1926, in Anderson County, Kansas, and it is the opinion of Dr. Edward H. Taylor of Kansas University that they were newly hatched.

Through the courtesy of Dr. Taylor the writer is able to present data gathered on an expedition of the Kansas University Biological Survey to Arkansas in 1926. Egg sets found are recorded as June 20, nine eggs; June 25, two sets of nine eggs each; July 2, nine eggs; and July 13, ten eggs. No newly hatched young had been seen as late as July 22.

The food of the *E. fasciatus* consists largely of insects and spiders.

Distribution in Kansas.—This lizard is evidently confined in its distribution to the eastern half of Kansas. It does not occur in rocky ledges of the prairie as does

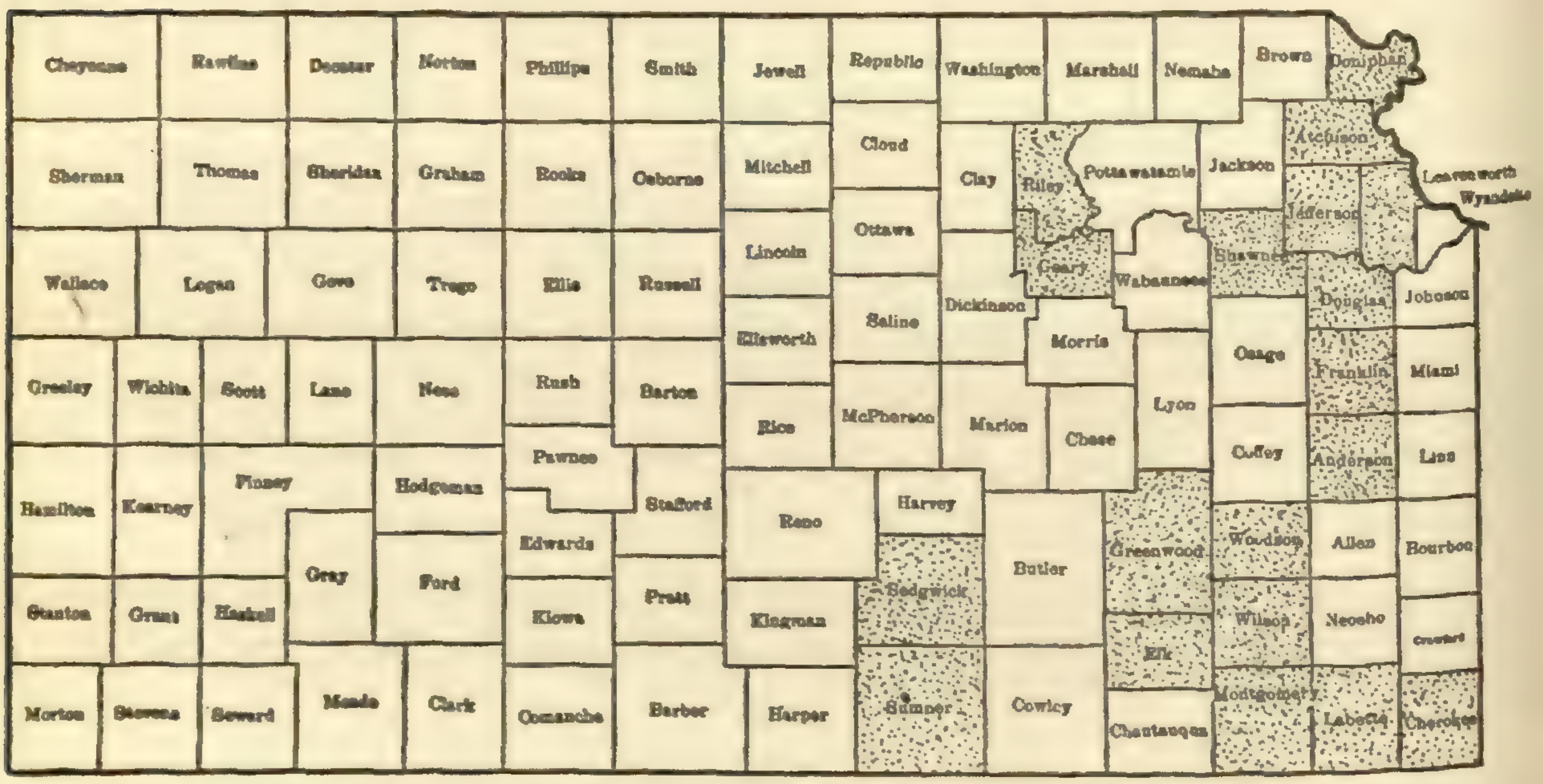

Fig. 11. Distribution of *E. fasciatus* in Kansas as indicated by the county reports.

E. obsoletus, and in addition sandy areas, chalk beds, and grass lands do not harbor it. Thus, the five-lined skink is apparently confined to the protection of thick woods.

Eumeces multivirgatus (Hallowell)

Many-lined Skink, Hallowell's Skink, Hayden's Skink.

Description.—Body moderately slender; ear opening

small; all scale rows on body longitudinal; legs rather poorly developed.

Back with seven or more brownish, almost obsolete stripes; vertebral stripe widest; dark bands bordering pale stripes; some of the light stripes very narrow, and others wider, more prominent; dorsal ground color distinct grayish brown to olivaceous; abdomen grayish; under parts of extremities, head and tail, all lighter; tan to whitish; differential coloration evident in dorsal scales of larger specimens.

A many-lined skink from Greeley, Colorado, has been measured. It has a partly regenerated tail, so only an incomplete set of data can be given from it. The body is 55 mm. in length, and the head width is 7 mm. The width of head expressed as percentage of body length is 12.7. Pratt (1923) listed the tail as "Three-halves length of body," a measurement that gives a tail percentage of 60.0.

Discussion of Kansas Reports.—The writer has never seen a Kansas lizard of this species, so takes this opportunity to present the records upon which he has admitted it to the state faunal list. In a letter dated September 9, 1926, Dr. L. Stejneger wrote that "In 1915 and 1916 Mr. V. H. Housholder sent me some Kansas skinks for identification. One from Labette County, I identified as *E. epipleurotus*, which I now consider as identical with *E. multivirgatus*. Another from Anderson County I identified as *E. leptogrammus*. This I also consider a synonym of *E. multivirgatus*." Although the writer has been unable to find these specimens in the present collection of the Kansas University Museum, he feels little hesitancy in listing *E. multivirgatus* as a Kansas species with the above identifications as the basis. The work of Cope (1900, p. 655) listed a specimen of

E. multivirgatus from Ft. Kearney, Kansas. In a letter dated January 3, 1927, from Miss Doris M. Cochran of the United States National Museum, the following information concerning this report is given "Regarding Cope's listing of *E. multivirgatus* from Ft. Kearney, Kansas, and soon after, *E. septentrionalis* from Ft. Kearney, Nebraska, Dr. Stejneger says that 'Kansas' is a mistake. The specimen is the type of *E. epipleurotus.*" Cragin (1881) listed a specimen of the many-lined skink from Neosho Falls, Woodson County.

Distribution in Kansas.—The distribution of *E. multivirgatus* in Kansas is at present confined to the eastern part of the state, but since specimens have been taken in Colorado, there is the possibility of its occurence further west.

Fig. 12. Distribution of *E. multivirgatus* in Kansas as indicated by the county reports.

Eumeces obsoletus (Baird and Girard).

Sonoran Skink, Common Gray Skink, Blue-Spotted Skink, Little White-Spotted Skink, "Black Skink," "Blue-tail Skink of Kansas."

Plestiodon obsoletum Baird and Girard, 1852, Proc. Acad. Nat. Sci. Philadelphia, 6:129 (type locality, "Valley of the Rio San Pedro, tributary of the Rio Grande del Norte, Texas").

Lamprosaurus guttulatus Hallowell*, 1852, Proc. Acad. Nat. Sci. Philadelphia, 6:206.

Description.—Head not well marked off from body; body elongated, largest diameter in center; tail long and tapering in perfect specimens; supraoculars large; tympanum easily seen in young, but sunken in the adult; ventral and dorsal scale rows longitudinal; lateral scale rows oblique as in *E. longirostris* Cope of the Bermuda Islands (unlike those of all other Kansas skinks); legs thick and shortened, especially in adults.

Coloration varies greatly between young and adult stages; *young* have been described as *E. guttulatus;* ventral color of young blackish, slate, or olivaceous; dorsal color coal black to light gray; back with or without five faint, almost obsolete lines; sides intermediate; tail brilliant blue; head scales usually shiny black; head and neck with white spotting; white spots on labials may be with partial, complete, or no inclosing black margins; head with or without white spot back of ear opening; neck with or without lateral white spots; as the specimen grows older, the coloration becomes lighter, the distinct white spotting on the head and neck is lost, and the dark scutellation, with special reference to that on the back, changes from scales with a solid color to those having a dark edge with a light spot in the center. Adult

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*The writer has just completed a manuscript on "The Synonomy, Variation and Distribution of the Sonoran skink, *Eumeces obsoletus* (Baird and Girard)," in which his reasons for this synonomy are set forth. This work is to appear in the Occasional Papers of the Museum of Zoology, University of Michigan.

ground color varies from blackish to light gray or olivaceous; ventral parts light to slate, often yellowish; lower labials and under parts of upper labials white or nearly so.

Data upon 150 Kansas specimens of *E. obsoletus* may be presented as follows: Length of body, 30-121 (91-100); length of tail, 36-168 (121-135); total length, 66-283 (226-250); width of head, 5-20 (14-16); length of tail as percentage of total length, 44.1-62.4 (56-58); width of head as percentage of body length, 11.8-19.5 (14-16).

Ellis and Henderson (1913) gave the total length of this species as 305 mm. This figure exceeds that of the writer, and equals the maximum figure given by Ditmars (1915). Other measurements are not given by these authors.

Habitat and Habits.—A survey of the literature shows that very little has been written on the habitat and habits of this form. Grant (1927) has discussed the behavior of a "blue-tailed" captive at some length. As indicated by studies in Kansas the Sonoran skink is able to live in a number of situations. It has been found in company with *Leiolopisma laterale* and *E. fasciatus* on thickly wooded hillsides in Douglas County, and with *Crotaphytus collaris* in Riley and Cowley counties situated in the vicinity of rocky prairie ledges above the wooded hillsides. In the spring of 1925, near the town of Haddam, Washington County, several specimens were taken from isolated outcroppings of sandstone where no trees were present. Specimens have not been taken in exclusively sandy areas, nor in the grassy Kansas prairie where there are no sheltering rocks. Six specimens were taken from limestone ledges near Haverhill, Butler County, in July. They were not found on the tops of the hills, but in the dips of valleys, where, no doubt, the soil humidity

was greater. One of these specimens was taken from under a rock in company with a medium-sized bull snake, *Pituophis sayi*, and two small sand snakes, *Tantilla gracilis*. In Ottawa County these Sonoran skinks were very active in a place called "Rocky Fern," an area of rocks, sand, and sparse vegetation. Here they were found associated with *Cnemidophorus sexlineatus* which was present in large numbers.

This species has been collected in Kansas from March 27 to October 9. It is one of the earliest lizards to come out of hibernation in the spring, and perhaps the earliest to hibernate in the fall, since fall collecting, as a rule, yields very few of them. The specimen which was taken on October 9 (1925), was buried about ten inches in the earth beneath a large rock, and was inactive when taken.

During the course of this study several copulation dates have been recorded for this species, namely, May 8, 1926; May 17, 1926; June 13, 1927; and June 15, 1927. The first two records are based on the same pair of individuals, but the last two are based on one female and two males. The copulation upon the second date lasted about four minutes. The act was preceded by a series of maneuvers, which ended in the grasping of a liberal fold of skin from the side of the female's neck, by the male, and the twisting of the latter's body beneath that of the female.

Eggs have been laid on June 18, June 26, and July 1, in Kansas. A female which was collected at Manhattan, Riley County, Kansas, on April 27, 1927, laid the following eggs in captivity at the Biological Station of the University of Michigan, Cheboygan County, Michigan: July 1, two; July 2, five; July 3, one; and July 7, one. This makes a series of nine eggs which were laid in the period of one week. The eggs were white in color when

laid and averaged about 11 by 18 millimeters in size. An adult female from Marshall County, Kansas, was dissected and found to contain fifteen eggs, the anterior one being lodged in a position between the front legs.

On August 13, 1926, the first blue-tailed young specimen was collected by the Kansas University Biological Survey in Cowley County, Kansas.

The Sonoran skink is a voracious feeder when in the open, and is very fond of caterpillars, grasshoppers and moths; however, it remains in concealment beneath the surface of the ground much of the time. In one instance a large male was observed devouring a recently laid egg of the species, taking it in his jaws and apparently swallowing it whole.

Distribution in Kansas.—Hurter (1911) did not report this species from Missouri, so Kansas is very probably on the eastern border of its range. The map indicates that the distribution of *E. obsoletus* is general over the state. As has already been stated, the Sonoran skink has been found in company with many other species of lizards, and is, perhaps, next to *Cnemidophorus sexlineatus*, the species with the most diversified habitats in Kansas. The difference in the type of habitat selected by the two species, *E. obsoletus* and *C. sexlineatus*, which are sometimes found together locally, can be explained as apparently that of soil humidity range, the skink being found in damper situations than the race-runner, though the general area occupied by each overlaps to a great extent as a comparison of their distribution indicates.

While making this study the writer has kept separate records for young skinks which might be identified as *E. guttulatus* from its original description, and has found that when reports of such lizards are plotted on a map,

they are in co-extensive distribution with the adult, *E. obsoletus*. The one exception to this synonymous occurrence is in Sumner County where only the *E. guttulatus* form has been taken. However, Sumner County lies next to Cowley County where a considerable number of adult specimens have been collected.

Eumeces septentrionalis (Baird).

Black Banded Skink, Northern Skink, Western Skink.

Description.—Body elongated, with longitudinal scale rows; legs moderately diminutive; coloration varies with age; young with two prominent light lines and two

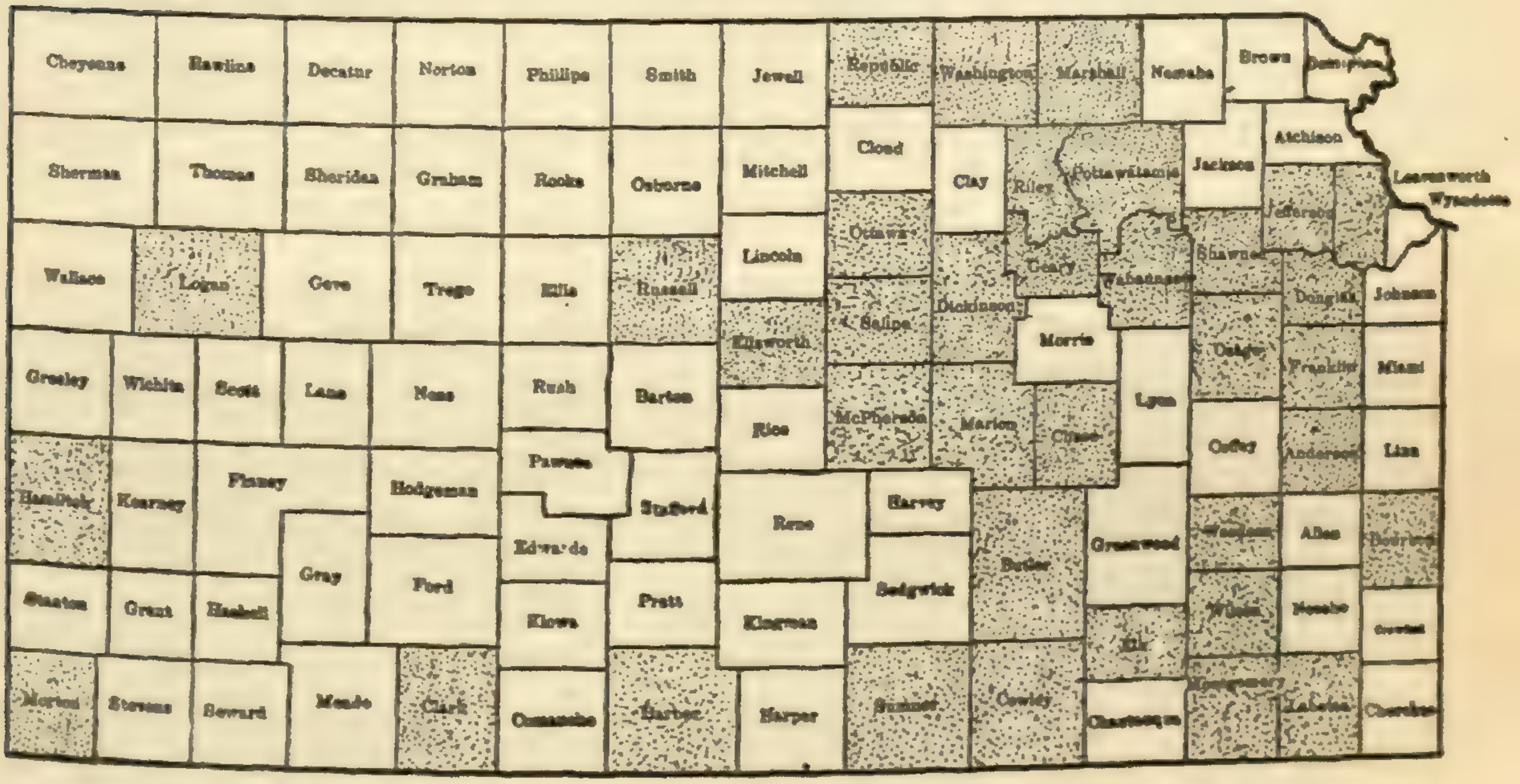

Fig. 13. Distribution of *E. obsoletus* in Kansas as indicated by the county reports.

or three dark brown bands on each side; wide mid-dorsal band of light brown present; adults with same number of stripes and bands, the general coloration becoming lighter with age; dorsal band between the two upper lateral dark stripes subdivided by two faint brown or blackish stripes into three light bands, one of which is vertebral in position; tip of snout salmon to light gray; ventral parts slate; lighter anteriorly.

The data obtained from 25 Kansas specimens are summarized below. Length of body, 34-78; length of tail, 69-124; total length, 108-202; width of head, 4-11; length of tail as percentage of total length, 60.0-71.2; width of head as percentage of body length, 11.8-15.9.

The writer has not found measurements given for this skink in the literature.

Habitat and Habits.—Very little has been written concerning the habitat and habits of this species. Ruthven (1910) stated that "It was found in the uplands and in the higher meadows, but only rarely. . . . Its principal habitat is undoubtedly the upland prairie." Over (1923) found that it lives in grassy places near thickets, but is difficult to see by the casual observer.

The author is indebted for some fine information concerning the Kansas habitat of this skink to Mr. F. F. Crevecoeur of Onaga, Pottawatomie County, Kansas, who has sent him a number of specimens with written accounts of their habitat and capture. Some extracts from his several letters follow. "While hunting ground beetles I have found as many as four of the northern skinks a day along a valley in a pasture about a mile from my home. Several times I have seen a specimen in my dooryard crawling through the grass near the path leading to the barnyard. I believe that it has made its home in the wood pile. . . . Some other places that I have seen this species, which is about the only one that occurs around here, are under stones in a dry creek bed; along a timbered creek under stones and at the foot of a stony hill which was at the side of a narrow piece of bottom land. . . . I remember seeing one on the upland at the edge of a cornfield that I was cultivating. . . . I am sending you a skink today that I took this morning while I was digging in my dooryard."

Mr. Crevecoeur collected fifteen specimens of *E. septentrionalis* about his home in 1926. It is of unusual interest that this lizard, so rarely taken elsewhere, should be found in such abundance in this one locality.

Prof. Felix Nolte of St. Benedict's College, Atchison, Atchison County, Kansas, has also kindly given the writer information about this lizard. He wrote on April 22, 1926, that "A specimen collected about April 17 was brought into a house in the western part of the city (no woods near), by a common house cat." The specimen was

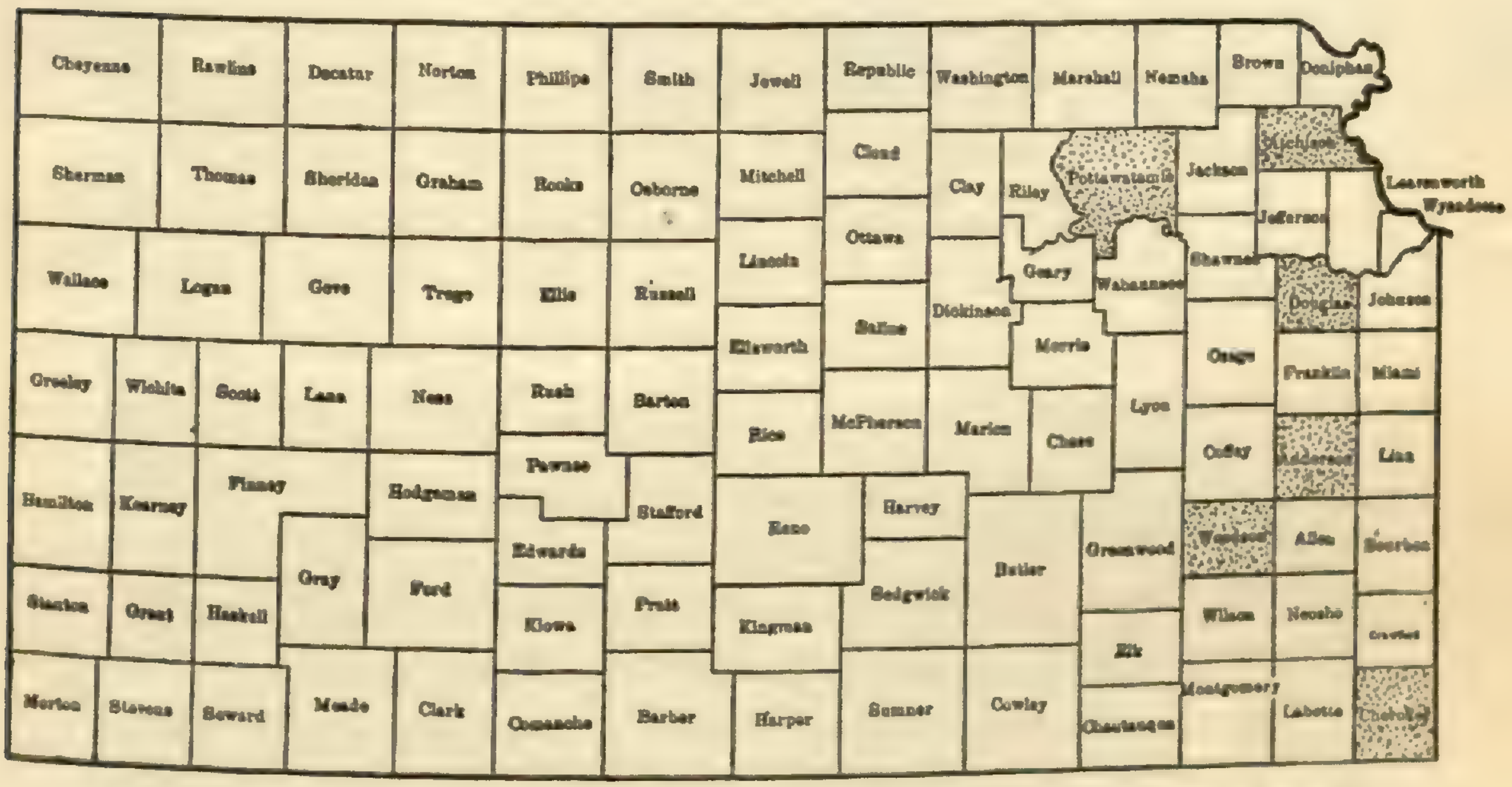

Fig. 14. Distribution of *E. septentrionalis* in Kansas as indicated by the county reports.

sent to the writer and when it was examined the teeth marks of the cat were still on the scales. The animal was alive and was kept in captivity for some time after it was received. On June 9, 1926, Prof. Nolte wrote another letter which explained that a second skink had been captured in precisely the same manner as the first. An examination of this specimen revealed a deep laceration in its back.

The black banded skink feeds upon a large variety of small insects.

Distribution in Kansas.—Eumeces septentrionalis is apparently an eastern Kansas form, and has not yet been found west of the distribution of *E. fasciatus*, with the range of which its known distribution in Kansas coincides. The distribution indicates that it may be confined to moist grass land and woods.

General Discussion.

Of the species of lizards discussed in the preceding pages the following are regarded as established members of the Kansas faunal list. Except in the case of *Eumeces multivirgatus*, specimens of each have been examined and identified by the writer: 1. *Crotaphytus collaris* (Say); 2. *Holbrookia maculata maculata* (Girard); 3. *Sceloporus undulatus thayerii* (Baird and Girard); 4. *S. undulatus undulatus* (Latrielle); 5. *Phrynosoma cornutum* (Harlan); 6. *P. douglassii ornatissimum* (Girard); 7. *Ophisaurus ventralis* (Linné); 8. *Cnemidophorus sexlineatus* (Linné); 9. *Leiolopisma laterale* (Say); 10. *Eumeces anthracinus* (Baird); 11. *E. fasciatus* (Linné); 12. *E. multivirgatus* (Hallowell); 13. *E. obsoletus* (Baird and Girard); and 14. *E. septentrionalis* (Baird).

The existence of data which might be made into Kansas reports for two species which are generically unrelated to all lizards definitely reported from Kansas in the above pages, makes their consideration here a necessity.

Although Ellis and Henderson (1913) in their work on the "Amphibia and Reptilia of Colorado" (p. 119), gave a table in which *Dipso-saurus dorsalis* was included among species recorded from Kansas, the writer's examination of over 1700 Kansas lizards has failed to reveal any of these specimens. This is significant when one considers that so conspicuous a form as the keel-backed lizard could scarcely be long overlooked. In order

to get a better understanding of this Kansas report a letter was written to Prof. Junius Henderson of the University of Colorado, one of the co-authors of the work in which it was printed. Prof. Henderson replied on September 14, 1926, that "Although most of the records in that paper which were based on previous reports were furnished by me from the card index which I had prepared, the table was made by Dr. Ellis. I do not know where he obtained the Kansas record, as we have no specimens of the form from there or elsewhere, and I do not find any reference to the record in either our species index or Kansas index." Another letter, asking for information concerning the basis of the report in question, promptly written to the co-author, Dr. Max M. Ellis, now of the University of Missouri, has as yet been neither returned nor answered.

In short, it may be stated that the established range of the species has never included Kansas; the lizard is absent from Kansas collections; Prof. Henderson is unable to substantiate the report; and Dr. Ellis has offered no objections to the questioning of his printed record. Therefore, it seems evident that the report was very probably a mistake, and that the species, *Dipso-saurus dorsalis,* should not be regarded as belonging to the Kansas fauna.

Although there are various rumors concerning the discovery of the gila monster, *Heloderma suspectum,* in Kansas, there is only one apparently authentic report of its capture in the state. A farmer, Mr. Gus Brune, Jr., who lives seven miles northwest of Lawrence, Douglas County, is said to have captured a large specimen in his hay barn on September 26, 1924. The creature was active and free when taken. It was given to the Kansas University Museum by its captor, and remained there

in captivity for some time. Finally it was killed and skinned. Its skin was preserved and is now a part of a fine collection of lizard skins kept at the Kansas University Museum.

The gila monster is the only poisonous lizard in the world, so far as is now known, and it is regarded with great concern in areas where it occurs. It is a brightly colored orange and black lizard of large size. It is so conspicuous a form that it would often be seen in Kansas if it normally occurred there. A theory has been advanced to explain the presence of the lizard in the hay barn mentioned above. Since the barn is only a quarter of a mile from the Union Pacific railroad track, it is thought that the lizard must have been carried into the state by the train, and escaping from its place in some car, made its way to the point at which it was later found. That the gila monster, *Heloderma suspectum*, does not normally occur in Kansas is accepted without question. A discussion of this lizard is included here only because of its special interest.

The records which have given the following species position upon the Kansas faunal list are regarded as very questionable, and the present data indicate that they are not to be considered as inhabitants of the Kansas area. 1. *Dipso-saurus dorsalis* (Baird and Girard); 2. *Holbrookia maculata lacerata* (Cope); 3. *Phrynosoma brevirostre* (Girard); 4. *P. douglassii hernandesi* (Girard); 5. *Cnemidophorus gularis* (Baird and Girard); 6. *C. tessellatus* (Say); and 7. *Heloderma suspectum* Cope.

From the standpoint of animal dispersal Kansas occupies a unique position. Adams (1902) has stated that

there have been two great centers of biological dispersal for the United States. They are the "Southeast and the Southwest, the former moist, the latter arid." Ruthven (1908) wrote that "Most of the forms which inhabit the prairie region either extend into the eastern forest region or into the plains region, or rarely both, few being confined to the prairie region. . . . There is a great difference in the extent to which the forms of eastern North America push westward, or the plains forms push eastward into the prairie region before becoming modified or checked." Thus it is found that dispersal after the glacial period has been from the southeast and southwest toward the central region of the United States in which Kansas is located. Since the two regions are opposed to each other, the line of their meeting must be somewhere in the central region, the distribution of each species being limited by its ability to withstand conditions more typical of its opposite region of dispersal, and less typical of its own region. The difference in the extent of the toleration of each species for the opposite region varies, as data on Kansas lizards show, and no distinct line can be drawn to mark the point at which the species with their center of distribution in the eastern region cease to exist and where the species with their center of distribution in the western region begin to appear. Thus, at the line of meeting there is an overlapping between the two groups, and it is in such a region that the factors limiting distribution are to be sought. If moisture were uniform at the point and temperature varied, temperature would be a controlling factor. If the formations of the area were geologically varied some of them would probably be preferred by certain lizards and some by others. Pearse (1926) has stated that "The distribution of animals often has direct relation to the

availibility of food, and particular foods are the leading factors in the lives of many animals.'' Most lizards are predaceous and take live foods, and since that is true, it is evident that factors which influence the distribution of the prey of the lizard, more or less directly, influence its own distribution. It is evident that the problems arising in such a region are both extremely complex and interesting.

Kennedy (1917), considering the general surface of the land, rather than its extremely varied texture, has written that ''Topographically Kansas presents little that is not monotonous. The eastern third of the state is a region of low hills, and meandering, muddy streams. The western two-thirds is an upland plain. The surface of the state rises gradually from 800 feet elevation in eastern counties to 3600 feet in Greeley County on the extreme western border of the state.'' The rise in elevation in the eastern half of Kansas is only about 700 feet, whereas the rise in the western half of the state is over 2000 feet. From this it is evident that Kansas is lower and flatter in the east than in the west. The topography of the eastern part of the state consists of rolling prairies broken frequently by wooded streams. Beginning at about the 1500 feet contour there is a rise to a treeless plain in the west. It is at this contour, theoretically, that the eastern and western regions meet. This is the place where the woods become sparser, and the rolling prairie extends onward. The above distributional maps show it to be a critical region in animal dispersal.

Precipitation, according to the Weather Bureau, United States Department of Agriculture (1923) decreases with remarkable uniformity from 42 inches in the southeastern counties to a little more than fifteen

inches at the western boundary. The northern half receives practically the same amount of rainfall as the southern. The eastern part of the state thus presents a much more humid surface soil than the western part of the state, another factor that has a profound influence upon lizard dispersal.

Only three of the fourteen established species of Kansas lizards have a state wide distribution. *Cnemidophorus sexlineatus* is one of the most widely distributed lizards in both the United States and Kansas. It is common to both eastern and central faunal lists. *Phrynosoma cornutum* and *Eumeces obsoletus* are also state wide in their distribution, but have come from the southwest beyond the plains of Kansas. Hurter (1911) reported only *P. cornutum* from Missouri, and Hurter and Strecker (1909) reported neither species from Arkansas.

Crotaphytus collaris occurs both to the east and to the west of Kansas. Its center of distribution is decidedly in the west, California being on the western line of its dispersal and Missouri on the eastern. Its distribution in Kansas is peculiar since it has been reported from only the eastern two-thirds of the state.

The skinks, *Eumeces septentrionalis* and *E. multivirgatus*, have their center of distribution in the "central area" and do not occur far to the east or west of Kansas. The former is a north central form, and the latter a south central form, Kansas lying in the pathway of the distribution of each, and possibly being the southern boundary of the range of *E. septentrionalis*, since Ortenburger (1926 a-b-c) did not report it from Oklahoma. The nine species of lizards that are left, counting again *Eumeces obsoletus*, which has not been found east of Kansas, fall into two nearly equal groups and are listed

below according to their known distribution. In no case has the writer found an authentic report of a western form east of Kansas, or an eastern form west of it, and in all cases the known reports in Kansas, with the exceptions of *Crotaphytus collaris* and *Eumeces obsoletus*, clearly indicate each species to be either eastern or western in its center of distribution as a glance at the maps will show.

The four species with their present centers of distribution in the southwest are *Sceloporus undulatus thayerii*, *Holbrookia maculata maculata*, *Phrynosoma douglassii ornatissimum*, and *Eumeces obsoletus*.

The remaining five species, which have apparently come from the southeast are *Sceloporus undulatus undulatus*, *Ophisaurus ventralis*, *Leiolopisma laterale*, *Eumeces anthracinus* and *E. fasciatus*.

Lizards occur in varying abundance in Kansas both as species, and as representatives of genera and families. The families Iguanidae and Scincidae are represented on the state faunal list by six species each, both being rich in multiplicity of forms, whereas the families Anguidae and Teiidae are represented in Kansas by one species each. *Phrynosoma cornutum* is a species which has always been taken singly in Riley County, according to the records, but nine specimens were collected in one afternoon in Ottawa County and more were observed. It is not easy to classify lizards as to abundance, though some are distinctly rare species and others are very common. The following table classifies Kansas lizards by species according to the extent of their appearance in collected material, and gives a rough index to their relative abundance in the state, since common lizards are taken oftener than rare ones.

Table of Kansas Lizards.

Species	Number of Specimens in Collections Examined	Per Cent of Total
Crotaphytus collaris	400	22.52
Eumeces obsoletus	280	15.73
Holbrookia maculata maculata	215	12.07
Sceloporus undulatus thayerii	190	10.67
Cnemidophorus sexlineatus	185	10.39
Phrynosoma cornutum	145	8.14
Eumeces fasciatus	120	6.74
Ophisaurus ventralis	80	4.49
Leiolopisma laterale	55	3.09
Eumeces septentrionalis	42	2.35
Phrynosoma douglassii ornatissimum	40	2.24
Eumeces anthracinus	18	1.01
Sceloporus undulatus undulatus	7	0.39
Eumeces multivirgatus (See p. 57)	3	0.17
Total	1700	100.00

The five lizards at the top of the list are certainly very abundant where they occur in Kansas. The eighth, *Ophisauris ventralis*, is not, however, abundant in the same sense, and more than a few specimens of this lizard are seldom taken at once. Yet, because of its widespread distribution in eastern Kansas and its occurrence near both the Kansas State Agricultural College and Kansas University where much of the collecting of Kansas lizards has been done, it is represented in Kansas museums in fairly large numbers. *Leiolopisma laterale* has not yet been found to be abundant in Kansas, with the exception of Franklin County, and usually only one or two specimens are taken at a place. On the other hand, the much rarer species, *Eumeces septentrionalis,* has been

found to be very abundant at Onaga, Pottawatomie County, Kansas. *Sceloporus undulatus undulatus* is a rare Kansas lizard, but Mr. W. H. Burt has reported it as being abundant on a bluff of Shoal Creek, Cherokee County, where it was "very hard to capture."

Literature Cited.

Adams, Charles C. 1902. Southeastern United States as a Center of Geographical Distribution of Flora and Fauna. Biol. Bull. 3:115-131.

Allard, H. A. 1909. Notes on Some Salamanders and Lizards of North Georgia. Science 30:122-124.

Bailey, Vernon. 1905. Biological Survey of Texas. N. Amer. Fauna 25:1-222.

Baird, Spencer F., and Charles Girard. 1852. Characteristics of Some New Reptiles in the Museum of the Smithsonian Institution. Proc. Acad. Nat. Sci., Philadelphia, 6:125-129.

Baird, Spencer F., and Charles Girard. 1853. Reptiles in "Marcy's Exploration of the Red River of Louisiana in the Year 1852." U. S. War Dept., Washington, D. C., pp. 217-244.

Barbour, Thomas. 1919. Distribution of *Sceloporus* in Southern Florida. Copeia 70:48-51.

Bentley, Georgia H. 1919. Reptiles Collected in the Vicinity of Currant, Nye County, Nevada. Ibid. 75:87-91.

Bishop, Sherman C. 1926. Records of Some Amphibians and Reptiles from Kentucky. Ibid. 152:118-120.

Blanchard, Frank N. 1922. The Amphibians and Reptiles of Western Tennessee. Occas. Pap. Mus. Zool., Univ. Michigan, 117:1-18.

Blanchard, Frank N. 1925. A Collection of Amphibians and Reptiles from Southern Indiana and Adjacent Kentucky. Pap. Michigan Acad. Sci. Arts and Letters 5:367-388.

Burt, Charles E. 1927. On the Type Locality of the Horned Lizard, *Phrynosoma brevirostre* (Girard). Copeia 163:53-54.

Cahn, Alvin R. 1926. The Breeding Habits of the Texas Horned Toad, *Phrynosoma cornutum*. Amer. Nat. 60:546-551.

Cope, E. D. 1866. On the Reptilia and Batrachia of the Sonoran Province of the Nearctic Region. Proc. Acad. Nat. Sci. Philadelphia 18:300-314.

Cope, E. D. 1875. Check List of North American Batrachia and Reptilia. Bull. U. S. Nat. Mus. 13:1-104.

Cope, E. D. 1880. On the Zoological Position of Texas. Ibid. 17:3-51.

Cope, E. D. 1900. The Crocodilians, Lizards and Snakes of North America. Ann. Rept. U. S. Nat. Mus. for 1898, pp. 153-1270.

Cragin, F. W. 1881. A Preliminary Catalogue of Kansas Reptiles and Batrachians. Trans. Kansas Acad. Sci. 7:114-123.

Cragin, F. W. 1884. Recent Additions to the List of Kansas Reptiles and Batrachians, with Further Notes on Species Previously Reported. Bull. Washburn Lab. Nat. Hist. 1:100-103.

Cragin, F. W. 1885. Second Contribution to the Herpetology of Kansas, with Observations on the Kansas Fauna. Trans. Kansas Acad. Sci. 9:136-140.

Deckert, Richard F. 1918. A List of Reptiles from Jacksonville, Florida. Copeia 54:30-33.

De Kay, James E. 1842. Zoology of New York, or the New York Fauna. White and Bisscher. 3:1-404.

Ditmars, Raymond Lee. 1910. Reptiles of the World. Sturgis and Walton Co. pp. 1-273.

Ditmars, Raymond Lee. 1915. The Reptile Book. Doubleday, Page and Co. pp. 1-472.

Dunn, E. R. 1915. Notes on the Habits of *Sceloporus undulatus* (Latreille). Copeia. 19:9.

Dunn, E. R. 1920. Some Reptiles and Amphibians from Virginia, North Carolina, Tennessee, and Alabama. Proc. Biol. Soc. Washington. 33:129-138.

Edwards, C. L. 1896. Life Habits of *Phrynosoma*. Science. 3:763-765.

Edwards, C. L. 1903. A Note on *Phrynosoma*. Ibid. 17:826-827.

Ellis, Max M., and Junius Henderson. 1913. The Amphibia and Reptilia of Colorado. Univ. Colorado Studies. 10:39-129.

Franklin, Dwight. 1913. Color Changes in Collared Lizards. Copeia. 1:2-3.

Gadow, Hans. 1906. A Contribution to the Study of Evolution Based upon the Mexican Species of *Cnemidophorus*. Proc. Zool. Soc. London for 1906. pp. 277-375.

Givler, John Paul. 1922. Notes on the Oecology and Life History of the Texas Horned Lizard, *Phrynosoma cornutum*. Jour. Elisha Mitchell Sci. Soc. 37:130-137.

Grant, Chapman. 1927. The Blue-tail Skink of Kansas (*Eumeces guttulatus*). Copeia. 164:67-69.

Hahn, W. L. 1908. Notes on the Mammals and Cold Blooded Vertebrates of the Indiana University Farm, Mitchell, Indiana, Proc. U. S. Nat. Mus. 35:545-581.

Hallowell, Edward. 1852. On a New Genus and Three New Species of Reptiles Inhabiting North America. Proc. Acad. Nat. Sci. Philadelphia. 6:206-209.

Hallowell, Edward. 1856 a. Note on the Collection of Reptiles from the Neighborhood of San Antonio, Texas, Recently Presented to the Academy of Natural Sciences by Dr. A. Heerman. Ibid. 8:306-310.

Hallowell, Edward. 1856 b. Notice of a Collection of Reptiles from Kansas and Nebraska, Presented to the Academy of Natural Sciences by Dr. Hammond, U. S. A. Ibid. 8:238-252.

Harlan, Richard. 1825. Description of a Variety of *Coluber fulvius* Linn. and a New Species of Scincus, and Two New Species of Salamandra. Jour. Acad. Nat. Sci. Philadelphia. 5:154-158.

Harlan, Richard. 1829. Genera of North American Reptilia, and a Synopsis of the Species (Continued). Ibid. 6:2-38.

Hartman, F. A. 1906. Food Habits of Kansas Lizards and Batrachians. Trans. Kansas Acad. Sci. 20:225-229.

Hassler, William G. 1927. The Fence Lizard in the Hudson River Valley. Copeia. 163:48-50.

Hay, O. P. 1892. The Batrachians and Reptiles of the State of Indiana. Ann. Rept. Indiana Dept. Geol. and Nat. Resources. 17:412-602.

Hay, W. P. 1902. A List of Batrachians and Reptiles of the District of Columbia and Vicinity. Proc. Biol. Soc. Washington. 15:121-145.

Holbrook, John Edwards. 1842. North American Herpetology. J. Dobson. 2:1-142.

Holt, Ernest G. 1919. *Sceloporus undulatus* (Latreille) Feigning Death. Copeia. 72:64-66.

Housholder, Victor H. 1916. The Lizards and Turtles of Kansas with Notes on their Distribution and Habitat. Kansas Univ., Dept. of Zool., Master's Thesis (Unpublished). pp. 1-110.

Hurter, Julius. 1911. Herpetology of Missouri. Trans. Acad. Sci. St. Louis. 20:59-274.

Hurter, Julius, and John K. Strecker, Jr., 1909. The Amphibians and Reptiles of Arkansas. Ibid. 18:11-27.

Hyde, B. T. B. 1923. Copulation of Fence Lizards near Roaring Springs, Gloucester County, Virginia. Copeia. 123:107-108.

Jones, J. Paul. 1926. The Proper Name for *Sceloporus consobrinus* Baird and Girard. Occas. Papers Mus. Zool., Univ. of Michigan. 172:1-3.

Jordan, David Starr. 1899. Manual of the Vertebrates of Northern United States, ed. 8 p. 201.

Kennedy, Clarence Hamilton. 1917. The Odonata of Kansas with Reference to their Distribution. Univ. Kansas Bull. (Biol. Ser.) 18:127-160.

Latreille, P. A. 1802. Histoire Naturelle, Reptiles. 2:40.

Linsdale, Jean M. 1927. Amphibians and Reptiles of Doniphan County, Kansas. Copeia. 164:75-81.

Loding, Henry P. 1922. A Preliminary Catalog of Alabama Amphibians and Reptiles. Geol. Surv. of Alabama, Papers Alabama Mus. Nat. Hist. 5:1-53.

Ortenburger, A. I. 1926 a. Reptiles and Amphibians Collected in the Wichita Mts., Comanche County, Oklahoma. Copeia. 155:137-138.

Ortenburger, A. I. 1926 b. Reptiles and Amphibians Collected in the Arbuckle Mts., Murray County, Oklahoma. Ibid. 156:145-146.

Ortenburger, A. I. 1926 c. A Report on the Amphibians and Reptiles of Oklahoma. Proc. Oklahoma Acad. Sci. 6:89-100.

Over, William H. 1923. Amphibians and Reptiles of South Dakota. Bull. South Dakota Geol. and Nat. Hist. Surv. 12:1-34.

Pearse, A. S. 1926. Animal Ecology. McGraw-Hill Book Co. pp. 1-417.

Pratt, Henry Sherring. 1923. A Manual of Land and Fresh Water Vertebrate Animals of the United States (Exclusive of Birds). P. Blakiston's Son and Co., pp. 1-422.

Reese, Albert M. 1922. Egg-laying by the "Horned Toad," *Phrynosoma cornutum*. Copeia. 103:15-16.

Rhoads, Samuel N. 1895. Contributions to the Zoology of Tennessee, No. 1, Reptiles and Amphibians. Proc. Acad. Nat. Sci. Philadelphia. 47:376-407.

Richardson, C. H. 1915. Reptiles of Northwestern Nevada and Adjacent Teritory. Proc. U. S. Nat. Mus. 48:403-435.

Ruthven, Alexander G. 1907. A Collection of Reptiles and Amphibians from Southern New Mexico and Arizona. Bull. Amer. Mus. Nat. Hist. 23:483-603.

Ruthven, Alexander G. 1908. The Faunal Affinities of the Prairie Region of Central North America. Amer. Nat. 42:388-393.

Ruthven, Alexander G. 1910. Contributions to the Herpetology of Iowa. Proc. Iowa Acad. Sci. 17:198-209.

Ruthven, Alexander G. 1912. Directions for Collecting and Preserving Specimens of Reptiles and Amphibians for Museum Purposes. Rept. Michigan Acad. Sci. 14:165-177.

Schmidt, Karl Patterson. 1921. New Species of North American Lizards of the Genera *Holbrookia* and *Uta*. Amer. Mus. Nov. 22:1-6.

Schmidt, Karl Patterson. 1922. A Review of the North American Genus of Lizards, *Holbrookia*. Bull. Amer. Mus. Nat. Hist. 46:709-725.

Shufeldt, R. W. 1885. Probable Period of Gestation in the "Horned Toad." Science. 6:185-186.

Smith, W. H. 1882. Report on the Reptiles and Amphibians of Ohio. Rept. Geol. Surv. of Ohio. 4:633-734.

Speck, F. G. 1924. A Note on the Breeding Habits of *Sceloporus*. Copeia. 128:35-36.

Stejneger, L. 1891. Directions for Collecting Reptiles and Batrachians. Part E., Bull. U. S. Nat. Mus. 39:3-13.

Stejneger, L. 1893. Annotated List of the Reptiles Collected by the Death Valley Expedition in 1891, with Descriptions of New Species. N. Amer. Fauna. 7:159-228.

Stejneger, L., and Thomas Barbour. 1917. A Check List of North American Amphibians and Reptiles. Harvard Univ. Press. pp. 1-125.

Stejneger, L., and Thomas Barbour. 1923. Ibid. ed. 2, pp. 1-171.

Strecker, John K., Jr. 1908. Notes on the Habits of Two Arkansas Salamanders and a List of Batrachians and Reptiles Collected at Hot Springs. Proc. Biol. Soc. Washington. 21:85-90.

Strecker, John K., Jr. 1910. Notes on the Fauna of Northwestern Texas. Baylor Univ. Bull. 13:1-31.

Surface, H. A. 1907. The Lizards of Pennsylvania. Zool. Bull. Div. Zool. Pennsylvania Dept. Agri. 8:234-264.

Taylor, Edward H. 1916. The Lizards of Kansas. Kansas Univ., Dept. Zool., Master's Thesis (Unpublished). pp. 1-97.

Taylor, Walter P. 1912. Field Notes on Amphibians, Reptiles, and Birds of Northern Humboldt County, Nevada, with a Discussion of the Faunal Features of the Region. Univ. California Publ. in Zool. 7:319-436.

United States Department of Agriculture, Weather Bureau. 1923. Summary of the Climatological Data for the United States, by Sections: Sections 38 and 39. Reprint: Kansas. Washington, D. C, pp. 1-54.

Van Denburgh, John. 1897. The Reptiles of the Pacific Coast and Great Basin; an Account of the Species Known to Inhabit California, and Oregon, Washington, Idaho and Nevada. Occas. Papers California Acad. Sci. 5:1-236.

Van Denburgh, John. 1922. The Reptiles of Western North America. Vol. 1. "Lizards." Ibid. 10:1-611.

Wiegmann, A. F. 1828. Isis. p. 369.

Winton, W. M. 1914. An Examination of Blood-ejecting Horned Lizards. Science. 40:784-785.

Winton, W. M. 1916. Habits and Behavior of the Texas Horned Lizard, *Phrynosoma cornutum* (Harlan), I. Copeia. 36:81-84.

Winton, W. M. 1917. Habits and Behavior of the Texas Horned Lizard, *Phrynosoma cornutum* (Harlan), II. Ibid. 39:7-8.

Wright, Albert H., and W. D. Funkhouser. 1915. A Biological Reconnoisance of the Ofinokee Swamp in Georgia. I. Turtles, Lizards, and Alligator. Proc. Acad. Nat. Sci. Philadelphia. 67:107-139.

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THE SEX ATTRACTION AND RHYTHMIC PERIODICITY IN GIANT SATURNIID MOTHS

Phil Rau
and
Nellie L. Rau

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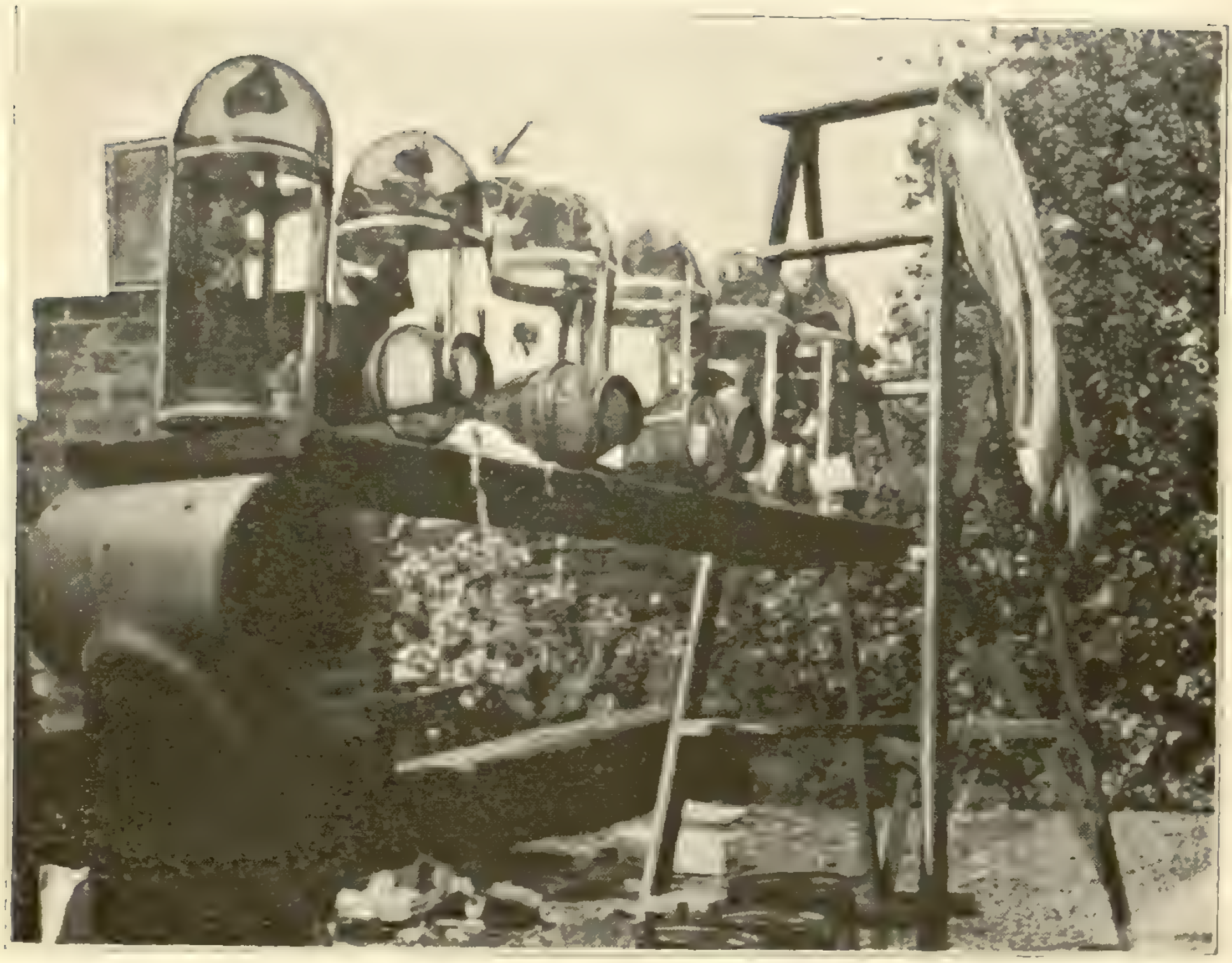

Fig. 1. Arrangement of cages on roof.

Fig. 2. A portion of the roof and view toward the west.

The Sex Attraction and Rhythmic Periodicity in the Giant Saturniid Moths

Phil Rau and Nellie Rau

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"With their tropisms, their rhythms, the adaptive manifestations of their differential sensibility—above all with their power of transforming habits into automatic actions—the articulates are essentially animals of instinct whose activities consist principally of automatisms, but automatisms dominated by cerebral power. One can hardly see in them 'simple reflex machines', for they know how to bend to circumstances, to acquire new habits, to learn and to retain, to show discernment. They are, one can say, somnambulists, whose minds awaken to give proof of intellect when there is need for it."—E. L. BOUVIER.

*"Instinct precedes intelligence both in ontogeny and phylogeny, and it has furnished all the structural foundations employed by intelligence. * * * Since instinct supplied at least the earlier rudiments of brain and nerve, since instinct and mind work with the same mechanisms and in the same channels, and since instinctive action is* GRADUALLY *superseded by intelligent action, we are compelled to regard instinct as the actual germ of mind. * **

*"We are apt to contrast the extremes of instinct and intelligence—to emphasize the blindness and inflexibility of the one and the consciousness of the other. It is like contrasting the extremes of light and dark and forgetting all the transitional degrees of twilight. * * * Instinct is blind; so is the highest human wisdom blind. The distinction is one of degree. There is no absolute blindness on the one side and no absolute wisdom on the other. Instinct is a dim sphere of light, but its dimness and outer boundary are certainly variable; intelligence is only the same dimness improved in various degrees. * * * Intelligence implies varying degrees of freedom of choice, but never complete emancipation from automatism. The fundamental identity of instincts and intelligence is shown in their dependence upon the same structural mechanism and in their responsive adaptability."—C. O. WHITMAN.*

PART I.

INTRODUCTION.

Night ever draws a veil of mystery about the things which belong to her domain. Although childhood's fear of the dark may have been explained away, yet the feeling lingers that in the realm of Luna we may expect something of the weird. Perhaps this, but more probably our love of undisturbed slumber, has led to an excess of fancies but a deplorable dearth of reliable information concerning the activities of these interesting denizens of our woods, the giant Saturniid moths.

Several years ago a well-known entomologist fascinated me with the story of how he had observed the males of the Saturniid moths "fly great distances up hill against the wind to reach the females." "How far," thought I, "can they actually travel, and what directs them there?" The question caught my fancy, and during the intervening years I have often thought of this "romantic" behavior. Often I was tantalized by seeing in the literature some meager references to this phenomenon, but while some authors suggested theories as to the guiding stimulus, none offered any experimental evidence as proof of any theory. Finally, bent upon an attempt to solve these problems of the sex life of the giant Saturniids, or more precisely stated, a study of how far the males can travel to reach the females, and what mechanical or psychical factors influence their reactions, I obtained a large number of cocoons of four species of these moths, to add to our native population here, and made detailed observations throughout the season.

The work was all done from the third story window and on the second story roof of the rear of the house, which could be reached from said third story window, of a city dwelling (fig. 2 shows a portion of this roof and view toward the west). At the windows and on the roof, from time to time, wire cages containing the female moths were placed. Then, taking a position of watchfulness, net in hand, I kept vigil through a greater part of the night, every night, from May 7 to June 27, a period of fifty-two days, which is the duration of the natural season for these species. Each moth was numbered, in oil paint, on the wings, and individual records kept of the age and activities of

each of the 1477 bred moths, and of the arrival and activities of each of the 1249 wild moths; thus the study comprises the individual records of 2726 moths.

While the problem involved many real difficulties and complications, yet the material held certain unusual advantages for such experimentation. These moths are easily handled, and have wings sufficiently large on which to paint distinguishing marks, so that accurate records may be kept of each individual. They require no food in the adult stage, so all adverse conditions arising from improper food are eliminated. By breeding the specimens from cocoons, accurate data may be had as to the age of the moths, and the factor of age in influencing their responses.

While this material came from Long Island, New York, three of the species, *Samia cecropia, Telea polyphemus and Callosamia promethea,* are natives of Missouri also. The fourth species, *Platysamia cynthia,* is not native of Missouri, but is abundant in the Atlantic States. Hence, in experimenting with the first three species, one had to contend with interference, sometimes favorable and sometimes troublesome, of the wild population hereabouts, but in handling the cynthias, we were certain that our imported stock constituted the entire population, although in some cases there was reason to believe that some of these moths responded slightly to the attraction of the females of the other species, and may thus have reduced the otherwise high percentage of returns.

The experiments could not be carried on just as they were planned; because of unexpected difficulties one could only take what material was at hand, quickly plan an experiment and execute it in the best way the conditions afforded. This factor may give the work a tone of not having been carefully planned. The difficulties were, of course, that often when one needed females, only males would emerge, and vice versa, and often a shifting of the wind, a change in the weather, and urban crowds, caused a change in a contemplated experiment. Extensive work, attempted two years later,* for the purpose of getting records of five-mile flights outside the city had to be abandoned because of the depradations of birds. Screech-owls devoured the incoming night fliers, and by day the sparrows, blue-jays and woodpeckers

*At Kirkwood, Mo.

attacked the prometheas in midair; in the morning the lawn was strewn with illegible, numbered wings.

Each experiment is a unit in itself, and is given as such. It was at first my intention to reduce the work to tables, and thus greatly shorten the text, but so many factors are involved in each and every experiment which would be lost in tabulation that it seems best to preserve these significant details.

HISTORICAL RESUME.

Everyone knows, in a vague way, that moths are nocturnal and butterflies are diurnal. While I can think of no instance of butterflies flying by night, we do know that some of the moths fly during the day.

There are few records on the actual hour of flight of moths of the family Saturniidae. To solve some of the problems of their flights it is not enough merely to know that the moths are active at night; it is necessary to know at what hour they fare forth. We have brought together here some of the chief items of information available in the literature.

Soule and Elliott[1] tell us that the promethea moth flies any time after two in the afternoon. Once a female at the window attracted forty males. Cecropia moths will fly near electric lights, and may be found under shed roofs by day, and may be tracked to their hiding places by their strong odor, especially strong in the females.

Possibly the most purposeful study of the sex activities in moths is that of A. G. Mayer.[2] He gives the results of experiments carried on in Florida upon material brought from Massachusetts. He finds that males are attracted to females not by sense of sight but by odor. A male will fly to a female even if his entire abdomen is cut away, and he will seek a female even when his abdomen is cut off and the sides of his thorax covered with impervious glue. From this he concludes that the spiracles are not the seat of the organs by which the male perceives the female scent. If the antennae are covered with glue, shellac, paraffin, photographic paste, etc., the moth no longer seeks the female, and will display no excitement, even though he be placed

[1]Caterpillars and Their Moths.
[2]Psyche, 9: 15-20. 1900.

within an inch of her. When the photographic paste is dissolved off in water, mating readily occurs. He also finds that blinding the males does not deter them from finding and mating with the females.

Fabre[3] writes quite spiritedly of the hordes of males that came to a captive female peacock moth. For a week they came to her each evening, between 8 and 10 o'clock. The first evening forty males arrived, and on another evening twenty-five came. Two years later he also got large numbers to come to his captive females which he moved about the house occasionally but did not succeed in deterring the males. He removed the antennae of some of these males, and his results and conclusions will be discussed later.

Fabre also experimented on a day-flying moth, the lesser peacock, *Attacus pavonia minor* Linn. From high noon until two o'clock each day for a week, the males came to the captive female, ten the first day and a total of forty for the week. He also observed that the moth known as the banded monk or oak-eggar attracted males from great distances at 3 o'clock in the afternoon in "very hot weather and brilliant sunshine," "coming from over the walls, over the curtain of cypress trees. The room is filled with a swarm of sixty males, keeping up their frenzied movements for three hours." With the banded monk he experimented by placing the females in loosely-put-together receptacles and in receptacles hermetically sealed. He found that the males discovered the females only in the loosely constructed receptacles, and not in the air-tight ones. He made tests also with a second species of monk moth, the clover Bombyx, nearly akin to the first, and plentiful about his home. He placed six females in cages, but not one male appeared.

Forel[4] says that a large swarm of *Saturnia carpini* came to his room in the city where he imprisoned females. The swarm of males that came outside to besiege his window was such that it attracted a crowd of ragamuffins in the street to catch the beautiful insects.

Kellog[5] gives us some valuable data on the silk-worm, *Bombyx mori.* He says the female moth, nearly immovable, protrudes a

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[3]The Life of the Caterpillar, Chap. XI. 1916.
[4]Senses of Insects, p. 76.
[5]Biol. Bull. 12:152. 1907.

paired scent organ from the hindmost abdominal segment, and the male walking nervously about and fluttering its useless wings soon finds the female by virtue of its chemotactic response to the emanating odor. Blind males find the females, but those with the antennae removed do not. If the female scent glands are cut off and put wholly apart from the female, the males are as strongly attracted to these isolated glands as they are to the unmated females. Males try persistently to mate with the isolated scent glands. Males mated with headless females and with females with the head and thorax off. Removing the left or right antenna of males caused them to move in repeated circles about the female, to the right if the left antenna was removed, and to the left if the right one was missing.

Duges[6] cut the antennae of two male (*Bombyx*) *Endea pavonia minor* and these insects were unable to find a female which they had previously been able to locate. Trouvelot performed various experiments on butterflies and on the promethea moth; he concludes that the antennae are the organs of smell. He regards it as a kind of feeling or smelling at a great distance by some process now entirely unknown.

Kirkland[7] experimented upon the moth *Prothetria dispar,* and found that the males were attracted to their mates solely by the odor of the females. He also found that the severed wings of the females were highly attractive to the males.

Mayer and Soule [8] conclude that it is not associative memory, but chemotaxis that attracts the males to the females of both *Callosamia promethea* and *Porthetria dispar.* They covered the antennae of the males with flour paste, and the moths did not again mate. In many instances, however, they did so immediately after the flour paste was dissolved away with water. In this same work the authors found that if the wind was allowed to blow from a female toward a male Saturniid moth of the same species, the male might be induced to mate with a female of another species confined in a cage with him.

Riley[9] liberated a male cynthia moth in the park a mile and a half from a female in his window. The next morning the two were

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[6]Quoted by McIndoo, Smithson. Misc. Coll. 63: 1-63. 1914.
[7]Quoted by Mayer and Soule, Jour. Exp. Zool. 3:429. 1906.
[8]Jour. Exp. Zool. 31:429. 1906.
[9]Insect Life 7:38-40. 1894.

together. Riley was much impressed by the attraction of insects for one another from a distance, and he tried to account for it by what is known in man as telepathy, for he says: "this power would depend neither upon scent nor upon hearing in the ordinary understanding of these senses, but rather on certain subtle vibrations as difficult for us to apprehend as is the exact nature of electricity."

Rau[10] describes the courtship of *Telea polyphemus* and says that during sexual excitement the antennae of the males are erect and alert, while on other occasions they are drooping and limp.

Soule[11] concludes from observations on *cecropia, promethea* and *angulifera* that there is some emanation from the ovipositor which attracts the male. The female protrudes the whole ovipositor which excites the males, and no male will mate or approach the female without being attracted in this way.

Hamm[12] while collecting Lepidoptera carried a bag in which a week previously he had confined a moth of *Bombyx quercus.* Several males of this species were attracted to this bag, and he attributed the attraction to the scent of the female still retained in the bag.

Von Dalla Torre[13] says the females of many Lepidoptera give out perceptible odors to the male and thereby induce copulation. It seems proven that by extending the ovipositor the female can cause the dissemination of odor which attracts the male.

Hauser[14] finds that *Saturnia pavonia* never makes an attempt to mate when the antennae are off.

Rau[15] shows that the female moths as well as the males display much emotion at mating time. When a male is introduced into the cage, the female often protrudes the ovipositor and gently or nervously moves the wings, thereby disseminating the odor, and brings him to great excitement. She sometimes chases him about the cage.

Fritz Mueller[16] says the males of many hawk moths can scent

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[10]Canad. Ent. 56:271. 1924.
[11]Psyche 9:226. 1901.
[12]Ent. Monthly Mag. 6:(31) 74. 1895.
[13]Quoted by McIndoo, loc. cit. p. 45.
[14]Quoted by Mayer and Soule, Psyche, 9:19. 1900.
[15]Trans. Acad. Sci. St. Louis, 20: 275-319. 1911.
[16]Butterfly Hunting in Many Lands. 1912.

the virgin females from incredible distances, and it has long been known that the privet and convulvulus hawk moths, especially during flight, diffuse a strong, musty scent. The males of a moth of the genus *Cryptolechia* and those of the *Glaucopidae* exsert from the apex of the abdomen two long, hollow filaments, from which proceeds a scent which is often very powerful to man. Similarly with the South American butterflies, the gigantic Morphos, the males extrude from each side of the apex of the abdomen a hairy, strong-smelling gland, of which the scent in *M. adonis* and *M. cytheris* resembles vanilla. In an interesting series of papers translated in this work, Mueller gives valuable information on the odor emitted by various species of Lepidoptera, and the precise location of the scent-bearing apparatus. On the relation of odor to sex attraction, he gives only the above information.

THE NUPTIAL FLIGHT.

Experiments on *Samia cecropia.*

Exp. 1. May 7. Two females emerged prematurely and for the past few days have been at the open window. This morning when I entered the laboratory I found that three young native cecropia males had come during the night and were quietly at rest on the window sash. Thus at the very beginning, the intrusion of the wild stock with the bred material complicated the observations.

Exp. 2. May 7. Wind, south-west; station, 225 yards east. Two of the native males that had appeared in Exp. 1 and a bred male 24 hours old, each with its distinguishing mark of paint, were liberated at 6:30 p. m., in the park, directly in front of the house; the caged females were on the window-sill. The air was humid from a shower that had just passed; the wind blew through the house, and there was a chance that it might disseminate to a point near to where these males were liberated. One hour and twenty minutes later, the bred male, one day old, came fluttering to the cages containing the females; no others returned.

Exp. 3. May 7. Wind, south-west; station, 225 yards west. The young male that had just returned in Exp. 2, was liberated at 8:05 p. m., of the same day, the same distance to the rear of the house, where the wind could not possibly waft the odors from our caged specimens. This moth did not return this time.

Exp. 4. May 7. Wind, earlier in the evening, had been south-west, now imperceptible; station, 225 yards east. Male 9 had emerged May 5, mated 7½ hours later, severed May 6, at noon; 30 hours later he was very active, and was liberated in the park at 9 p. m. The conditions were the same as in Exp. 2, excepting that the wind had fallen and this male had already mated. The temperature in the room was 68° F., while outside it was 59° F. After 40 minutes, he flew in the window and passionately fluttered about the cage; he did not stop at the cage in the window, but flew past it into the room and hovered about the younger female on the table.

Exp. 5. May 7. Wind, same; station, ½ mile east. This male which had just returned was taken out for a longer dis-

tance in the same direction, and liberated at 10:15; at 11:25 it returned again. The temperature was now falling; the large number of park lights which the moth had to pass seemed to exert no disconcerting influence.

Exp. 6. May 7. Wind, same; station, 1 1/6 mile east. Once more this weary moth was taken out to a more distant point in the same direction, and liberated at 11:50 p. m., but it never came back. The temperature fell low that night, with rain and snow, so we must abandon the experiment without knowing whether exhaustion, lack of odor perception, adverse weather conditions or the presence of some other female elsewhere caused the failure of this moth to return. Later tests proved that both rain storms and greater distances than this may be surmounted by these creatures.

Exp. 7. May 14. Four females of various ages had been kept at the windows for several days, and this morning 7 young native males were found in the room.

Exp. 8. May 15. While the east windows were closed, 12 native males flew in during the night through the west windows. However, they did not remain in the west room, but moved to the east room, probably attracted by the light rays of dawn more than by the odor of the females, for all were at rest on the window sash, instead of the cages on the table. Judging from the perfect condition of the wings, all were quite young.

Exp. 9. May 16. Since May 14 and 15 had given us 19 wild males, and I was in need of more material, I made special effort to get them by opening all the windows and placing to advantage (in relation to wind) my best females. But none came during that night. This inactivity may well be attributed to the low temperature, which was only 50° F., between 1 and 4 a. m. We know from earlier investigations* that a low temperature retards the activity of these creatures and, by conserving their stored energy, which cannot be replaced, prolongs their life. Heavy rains and thunderstorms occurred during the night also, but on other occasions these elements did not deter the moths in their flights when temperature conditions were favorable.

Exp. 10. May 17. With the thermometer fluctuating be-

*Trans. Acad. Sci. St. Louis. 23: No. 1, 1914.

tween 50 and 55 during the night, only two native males flew in at the window.

Exp. 11. May 17. Wind, south until 7 p. m., then shifted to east; station, 250 yards east. The two native males which had come in during the night, and two bred males, aged 4½ hours and 6 days respectively, were liberated in the park east of the house at 6:30 p. m. None of these moths returned that night, but three mornings later the youngest one was with native males that flew to the laboratory. It would be interesting, indeed, to know where and how he at last "hit the trail."

Exp. 12. The night of May 17-18 was chill and stormy; the temperature was about 56°, and almost an inch of rain fell between 7 p. m. and 7 a. m., while a strong wind blew from the east, through the upstairs windows. The two laboratory rooms had five windows, two opening directly to the east and three to the west. The two eastern windows contained 7 cecropia and 3 polyphemus females, and the western windows had 4 cecropia (1 dead) and 3 polyphemus females; all these had been in this position for two days, giving ample exposure for the dissemination of odors or any other means of communication which betrayed their presence. But the two nights preceding had brought in none, and even the cocoons on hand were yielding no moths; the beating rain foretold disappointment again, so, being dead for sleep, I retired at midnight.

At 4 a. m. I was startled awake by the beating of wings on the window-shade in my second floor bedroom, and the rasping rustle of many wings in the laboratory. Going to the third floor, three steps at a jump, I was met by dozens of excited cecropias flying about the cages on the west windows, and looking out I saw many more fluttering in my direction and making their way crookedly to the windows, all through the pouring rain. The females in the cages, heretofore always sluggishly quiet, showed great agitation, beating their wings against their cages. This shows that the females, too, join in the activity, or, as later experiments will show, by flapping their wings they disseminate the odor from their bodies. Excitement ran high as other members of the family, brought thither by their curiosity regarding the unwonted commotion at such an hour, forgot their sleepiness

and joined in the impromptu ghost-dance in an effort to capture the many giant moths that were fluttering and darting like bats about the ceiling and walls of the rooms. When, at last, the moths had ceased to come in and had all been gathered into cages, it was found that 42 had come in during this brief period. Standing on my roof as daylight was breaking over smoky St. Louis, and viewing my trophies in the cages, I can truly parody Emerson:

> A second crop thy roof-tops yield
> Which I garner in a yawn.

With these made safe, I could then calmly make records of the many interesting details which had been crowded into that brief period. This great movement of the moths had occurred just as day was breaking, at a little before 4 a. m.; by 4:30, they had entirely ceased to come in, and more than that, the moths in the cages had all subsided to quiet, and rested motionless. This was my first intimation that their activity is probably strongly periodical; henceforth I was always on guard to discover the factors controling this periodicity.

It was unquestionably evident, as I watched them coming in, that all of these males came from the west, flying against the wind. Not one of them flew to the east windows, where other females were in cages, neither did any of them fly over the housetop and retrace its flight. It seemed that the strong east wind blowing through the house must have carried the odors out through the west windows, and the males, following it back, came to the west windows instead of the east ones. Unless we consider this hypothesis, there is ample reason to expect more moths to come from the east than from the west, because the area to the west was closely built up with dwellings and industries, while to the east lay a large park. It seems to me that, even if no other tests were made, this one experiment would be sufficient to demonstrate conclusively that wind is a factor in bringing the males to the females. This is quite unlike Fabre's* observations of *Attacus pavonia minor*, which, he says, came with the wind. The seven females in the east windows attracted no suitors from without, but the four (one of which was dead) in the west windows drew the mob. Surely, had factors other

*Social Life in the Insect World, p. 197. 1912.

than the wind brought the message to the males, as Fabre thinks, then a fair proportion of them, at least, would have come in with the wind at the east windows.

As the first dim light appeared it was interesting to watch from the roof the flight of the approaching moths. They did not fly high in the air, on the level with the row of roofs, but approached the house flying near the ground, at the height of the shrubbery, and when they came near to the house that harbored the females, they would soar upward and bob up over the edge of the roof. This showed that if they were following the female odor, it did not disseminate in volatile fashion to heights above, but was heavier than air and dropped to lower levels, at least in this moist atmosphere. In later experiments, this low flight was rarely seen; the moths approached from a distance flying at about the height of the roof. Probably in this case the heavy atmosphere would not permit the female odor to disseminate freely, but had a tendency to force it near the earth.

Of the 42 newly captured males, only 3 had frayed wings, showing age; 39 had perfect wings with smooth pubescence and powdery scales in place, thus proving their youth. In fact, a number of them, when handled, ejected the chalky white fluid, a trait which is exhibited by these moths only soon after emerging. Their wings seem to be thoroughly waterproof, for although they came in through the pouring rain, none of them were wet or soggy.

One of these young males, as soon as it flew to the cage, was quickly thrust inside, to ascertain how much time would be lost, or rather spent, in courtship, before mating began. Within two minutes after he had entered the cage, mating had occurred and the pair was resting quietly.

Exp. 13. May 18. Wind, southeast; station, 1 mile northwest. The point of liberation was carefully chosen, as nearly as I could determine, in the direct path of the wind, but between the hour of liberation, 9 p. m., and the hour of their flight, at dawn, the wind changed and came directly from the south. Twenty-four native moths, captured at dawn that morning, were used in this test. These moths had been experimented upon in the glass box during the day (see p. 152) when the others had

been normally at rest, and the factor of fatigue should be considered in the results of this experiment.

The 24 marked moths had the following histories: 3 were old and had dilapidated wings, 1 was the young, wild male that had mated early that morning, and the remaining 20 were fresh young wild ones. Since the startling events of the night before had taught me that their regular time of flight is just before dawn, I began my watch at 3 a. m.; at 3:30 the moths began to arrive in great numbers, and at 4:30, before daylight was yet clear, their flight was at an end. The exact timing, the precision of their flight, seemed almost uncanny. We may well say " 'Tis the witching hour," until we can say something better, which, alas! we cannot yet do.

In that hour, 54 males were captured, but only one in the lot bore the marks which told that it was one of the 24 which had been taken out the evening before to a point one mile distant. But the story is not complete until we add that three others came in at dawn of the second day. This is easily explained, hypothetically, by mere chance; it is quite natural that as the 24 moths wandered in various directions, a few of them would, sooner or later, come by chance into the path of the wind from the house, and from there follow the trail home. All four of those which came in were of the lot of 20 young wild moths. Moreover, we must constantly bear in mind that, although in a wild state, the males regularly emerge somewhat prior to the females, by this time there were probably a few wild females in the woods to distract our experimental males from their course, for these moths have no "homing" interest which would draw them back to the house where they had hatched, as a bee or a wasp would have, but their only interest is the call of their mates in that house.

Exp. 14. May 19. Wind, south; station, ½ mile north. The 53 fresh young males which had come in at dawn were marked and liberated at 10 p. m. One must not lose sight of the fact that these had already made one flight, from an unknown distance, to the roof, and if they returned again it would be their second successful journey, which would be an advent of no small proportions in the life of a creature which lives only a few days. As in the last test, the point of liberation was chosen in the

direct path of the wind, but again the wind played tricks on us; at 12:30 it changed sharply and blew from the east, and by 3:30 it was from the north to the south, or just the opposite from what we wished. There was also a thunderstorm. The period of their arrival that night was from 3:33 to 4:40 a. m., during which time 39 males came to the cages. Five of these had been liberated six hours previously; one had been taken out two days before, and the other 33 were all young wild moths. It seemed to me that these six experienced fliers found the cages more quickly, alighted more quietly and did not spend so much time in wild fluttering as did the first time fliers. That would be quite natural, since they were older and more experienced. The dawn of the following day brought in 9 more marked moths of this lot, and even two days after that (May 22 and 23), one each. Thus, out of 53 males liberated, 16 eventually returned, even amid variously shifting winds. However, the majority of them were out for so long a time that their return need not be regarded as any more significant than the arrival of any other aimless wanderers in the woods and shrubbery.

Exp. 15. May 20. Wind, imperceptible; no leaf was stirring; station, ½ mile east. The 39 males, including the 6 which had already made two flights to the roof, were now duly marked and taken out into the park at 10:30 p. m. During the regular period of flight the following dawn,* 93 males came in; of these 89 were newcomers, one had come to the roof the day before, and 3 were members of the lot of 6 that had made two previous flights to the roof! That proportion is too large to be passed by unnoticed, or to be attributed to mere chance (especially with the wind unfavorable) when contrasted with the much larger number of other moths which had exactly the same chances but less experience. Shall we suspect that these individuals were naturally endowed with a higher degree of sensitiveness or ability than their fellows, or that their superior success was the result of profiting by experience? Is it possible that these, too, would have failed without something akin to place memory? It is possible also that those of subnormal ability were eliminated in the first flight, and those taken on the second flight possessed superior sensitiveness to stimuli. One out of the remaining 33

*In this case, at dawn the wind was blowing from the south.

was not the entire result of the test of the younger ones, however; on the following morning 10 more arrived. This only shows that those which had had only one previous experience in coming to the roof were unable to repeat the performance in unfavorable winds, but probably had to wait until the winds shifted to a favorable direction or until, in their wanderings, they came into the path of the breezes.

Exp. 16. May 21. Wind, northeast; station, ½ mile south. The 36 males used in this test were all young wild ones which had come in at the dawn of that day. At dawn, or to be exact, between 3:30 and 4:05 a. m., on May 22, 4 of these came in, and on the two following mornings two and three came in, or a total of 9 out of 36 in the three days.

Exp. 17. May 21. Wind, northeast; station, 1 mile south. The setting for this test was the same as for the last, excepting that the distance was greater; here, too, the moths were not liberated in the direct path of the wind, but to one side of it. Of the 36 set free at 7:30 p. m., 2 came back the following dawn and one on the third morning.

Exp. 18. May 21. Wind, northeast; station, ½ mile south. The time, place and wind were again the same as for Exp. 16, but the material was all bred males, six of which were two days old, one was one day old, and the other was a bred male which had successfully returned in Exp. 11, and was now seven days old. The last one came back the next morning, but the others were all permanently lost.

Exp. 19. May 21. Wind, northeast; station, ½ mile south. Eleven experienced moths were liberated in the evening under precisely the same conditions as in the three preceding tests. These, which had already made two flights to the roof, were given special colored markings, to distinguish them from the common stock. A few hours later, at dawn, five of these reappeared at the laboratory. Really, now, it is difficult to restrain oneself from jumping to conclusions, or at least from entertaining conjectures, when we briefly summarize the data from these last four experiments. All were exactly parallel as to time, place and weather. The wind was only partially favorable; it was blowing toward the south-west, whereas to be favorable it should have been directly toward the south, but this condition

obtained for all alike. I hold that we are logical in assuming in all these tests that those which came in one and two days late did so only by virtue of their wanderings or of shifting of the winds, and hence do not have much weight in the present investigations. Out of 72 new males which had flown to the roof from their wild haunts, 6 came back in this test flight (6 more came in on following days); out of 7 young bred males which had never been out of doors before, none returned; one bred male which had made a successful previous flight did come back, and out of the lot of 11 which had made two previous flights, 5 came in promptly. All that we dare say at this point is this: while we have tried as far as possible to eliminate complicating factors, our problem is still a tangle. In this tangle we can from time to time recognize threads of different kinds, but the wisest method for us is to follow up and straighten out the one thread with which we have begun; in that way the others will be more easily disentangled later. The element of chance is always present to complicate matters, but here we are about to become involved with the factors of profiting by experience, and possibly trial and error; later we shall meet the more obvious but less knotty obstructions of old age and fatigue. The only kink conclusively disposed of here is that about 20 per cent of these moths can follow the trail of the female for a half-mile when the wind is semi-favorable.

Exp. 20. May 22. There was a dearth of female cecropias; it seems, as Fabre complains, "when the farmer needs dung, the asses become constipated"; now when I so needed a few females, only males emerged. I even went so far as to put cocoons in the incubator, but when they came forth, they were males and more males. Let us take inventory of our stock of females and estimate their drawing power. In one cage at the window were seven dead females and one feeble one nine days old; this cage had not been attractive to the opposite sex for the past two nights. In another window were four, aged 10, 8, 8 and 3 days; other experiments have shown that 2 and 3 days is the most attractive age; therefore for the approaching dawn the burden of attraction lay with this young moth. I waited with curiosity, and at 3:25 the first suitor arrived; they came on constantly in groups or singly until 4:30, the usual time for the procession to

end. To my astonishment, the greatest number that ever flew to the roof were captured; four large cagefuls, or 119 moths, and about 20 evaded capture in the rush, making a total of 139! Of these, 93 were new native males, and 26 wore color markings which showed that this was their second or third flight to the roof. (The returns of these are recorded under their respective experiments.) This gives us the surprising evidence that a few females exert as potent a power of attraction as many.

As I stood on the roof peering into the darkness to see whence they came, I soon found that they were not coming from the north or west, where the vista was open, but the majority of them bobbed up over the mansard of my house and the house on the south, but they did not come in through my east window; this indicated that they were coming from the southeast. In my restricted position I could not determine with certainty the direction of the wind, until I noticed that the light smoke from a tall chimney a block distant floated away toward the southeast in an unbroken ribbon. Here at last was convincing evidence to justify my long surmise that they are guided to their goal by the wind, and hence follow back against the current of air which brings them the message.

Exp. 21. May 22. Wind, northeast; station, 2 miles southwest. Fifty males were taken out on this test flight; 44 were wild ones which had come in that morning, and 6 inexperienced bred moths (3 were 1 day old, 1 was 2 days and 2 were 3 days). I tried to place them, as nearly as I could estimate, in the path of the wind, at the distance of two miles. None returned the next dawn, but on the following mornings one each came in. Two miles was a long distance to exact of them, but since others in later tests accomplished more than that, I cannot explain this almost total failure, unless it be that the chances were thereby greater for them to miss the direct current in the wind, or, more probably, for them to meet native females en route.

Exp. 22. May 23. Twenty-seven native males which had come in the day before were marked and liberated at 2:30 a. m. in the darkened room, to see if at close range they would settle on the cages of the females. The only females in my possession at that time were the aged and worn ones mentioned above, but later tests proved that they were still capable of exerting their

attraction. The females were in the west windows, and the wind from the northeast was blowing in at the east windows, so the wind passed over the males first and touched the females later. After an hour the males were found fluttering, and when the lights were turned on, they fluttered violently about the lamps, but they did not approach the cages; they wandered out of the windows instead. Of course the males' agitation cannot be attributed to the presence of the females, because at this hour, 3:30 a. m., they always become active. After watching them for some time I was convinced that they registered no reaction to the females near by in this position, and when they wandered away I did likewise. On the morning of the following day I found 10 of these marked moths clinging to the cages of these females. I have no record of the wind throughout the night, and do not know whether their eventual success was due to shifting breezes, their aimless wanderings, or some other cause.

Exp. 23. May 23. In Exp. 20, I describe the dearth of females, and the marvel that so many males should react to a few aged specimens and a single young one. Even these were now a day nearer the grave, and not a new one had appeared to replenish the stock. The cages were watched from 3 to 4:30 a. m., but not a native male came to them. During the entire period, only 3 came in, and these were marked ones, which have been recorded in a previous experiment. Was this due to the fact that these females had become so impoverished as to be impotent to exercise their attraction, or can it be that the unusual influx of native males at the previous dawn had included about all the stray males in the region? I can hardly imagine the latter to be true, since I saw the moths coming in from only one quarter of the compass. The three which did come in had made successful flights previously, but again one cannot tell whether, because of their experience or superior sensitiveness, they could react to weaker female emanations, or whether they were aided in their return by something akin to place memory.

Exp. 24. May 23. Wind, east; station, 30 feet west. The test on the preceding evening indicated that the males cannot find the females, even in close proximity, if the wind is blowing in the wrong direction. Now we liberated at 8 p. m. 23

native males (19 new ones, 2 which had made two successful test flights and 1 which had made one test flight), 30 feet west of the windows where the females' cages were, and on the ground about 25 feet below them, with the wind blowing from the females toward them. Males of this species have the ability to fly long distances when the wind is favorable; can they make a successful flight for a short distance, or is proximate orientation more difficult than distant orientation? In the bright moonlight between 11 and 11:10, three males came in; at 12:05 a fourth one; and between 3:05 and 4, six more, all of which had been taken out for their first test, and the one which had made one successful previous test. Here we see that 11 out of 23 males can find the females at a short distance when the wind is right, even if the females are aged and decrepit and only three in number. Some of these males came in before the usual hour of dawn; these were undoubtedly influenced by the bright moonlight, but if four were so influenced, why were not all? In an experiment with females on the ground and also on the roof, I had found approximately an equal number of males coming to both places, showing that odor trail can be followed by the males regardless of such an elevation.

Exp. 25. May 24. During the day, two females emerged, and these with the three old ones were placed in the windows. Two males appeared at 3:05 and 3:10, a little earlier than usual, and between 3:25 and 4:30 71 came in and were captured, and about ten evaded capture, making a total of 83 which responded to the attraction of these females. A census of these 73 revealed 48 wild ones, of which 25 were young and 23 old and worn, and 25 bearing our marks, proving previous flights. This is a larger proportion of old ones than had been seen on other mornings, and the fact that old ones came in also shows that they must have been in existence and probably would have responded when they were young if the female attraction had been sufficiently strong. This circumstance also shows beautifully why so few old males came to the roof. The reason is that they all respond while they are young. It also shows that when the female attraction is too weak to lure them, they can still respond when they are old when they meet it later in life. During the influx the moths could be seen coming from the west and southwest; the wind was from the northeast.

Exp. 26. May 24. Wind, east; station, 15 feet west. At 11:50 p. m. five males were liberated at the edge of the roof 15 feet from the females, and with the wind blowing directly upon them from the cages. Three of the five flew to the cages at 3:25, 3:40 and 3:55 a. m. This shows clearly that they can orient themselves, even if the distance is short. But more interesting is the evidence that, despite the fact that the cages were only 15 feet away, the moths did not fly to them until dawn, the precise moment of their customary flight, almost four hours later. This demonstrates, of course, the dominance of a standard rhythmic periodicity, but since the moths sometimes react to moonlight, one suspects that this periodicity is not regulated by the clock, but by a condition of light which acts as a stimulant. There was no moon that night. Later experiments show that when the moon is bright they sometimes fly to the females without waiting for the streaks of dawn to act as a stimulus.

Exp. 27. May 25. One more female cecropia had emerged, while some of the dead ones (functionally speaking), had died, so this dawn found three young females and one old one displayed in my windows. These attracted 42 moths from 3:30 to 4:30 a. m.; this was about half of the number that had come in on the preceding day when fewer young females were present. This shortage may be explained by either the deficiency of the wind, or the probability that yesterday's response had drained the population. Sometimes no wind was perceptible, and again there was a faint breeze shifting from one direction to another. It may be that returns are better when the wind is stronger, for that would clear away the city's smoke and carry the emanations more directly. Of the males captured, 41 were native newcomers (26 old and 15 young); one bore a mark showing that he had come (at this late date) from a two-mile point, as recorded in Exp. 21 on May 22.

Exp. 28. May 26. I fell asleep that night, and instead of going on watch at 3 o'clock as I had planned, it was 4:20 when I hastened to the third floor. The rain, which had been falling heavily all night, continued. I found a dozen males fluttering about the room, and in all probability many had come and gone in my tardiness of fifty minutes. However, on account of the rain the light conditions were less intense at 4:50 than they

usually were at 4:30 on clear mornings, and instead of the flight stopping at the usual time, it continued for twenty minutes longer, or until 4:50; this point is interesting in that it demonstrates how much a slave to certain intensities of light these creatures are. In all, about 20 males were taken, a small number, but sufficient to demonstrate conclusively that heavy rains do not deter their flight, and that after flying in the rain they are none the worse for wear. Since it had rained steadily from 7 p. m. to 7 a. m. (1.6 inches of rain fell), this flight shows that the rain does not obliterate their medium of communication (odor?). All of the males were native ones that had never been on the roof before. If one could prove that the action of this amount of rain could destroy the female odor or cause it to settle on or near the ground where it could not disseminate, and then if the males still flew to the cages, one would have to attribute the action to something other than odor.

Exp. 29. May 26. Wind, east; station, 30 feet west, on ground. This experiment and the three that follow (also Polyphemus Exp.) were conducted during the night of May 26-27, and are of especial interest because the moon shone for certain periods during the night and the irregular and unusual flight of the moths correlated beautifully with the periods of moonlight. The intricacies of their reaction to intermittent and constant moonlight will be considered in detail later in these pages. Fourteen male cecropias were liberated in the back yard on the ground, 30 feet west of the females, at 11:55 p. m., with the wind blowing directly toward them. Six of these came back, one at 12:05 (after only ten minutes), one at 1:25, three between 3:18 and 3:40, and the sixth one came in at dawn a day later.

Exp. 30. May 26. Wind, east; station, ⅛ mile west. Thirty new native males and one which had made two previous flights were liberated a little further west and three minutes later than the last lot. Thirteen of these returned, the first three arrived 22, 72 and 77 minutes after they were set free, nine came in between 3:40 and 4 a. m., and the experienced flier came in the next day at dawn.

Exp. 31. May 26. Wind, east; station, 1 mile west. Thirteen males from 1 to 3 days old, which had emerged from cocoons in

the laboratory, were liberated one mile west at 11:48 p m. Seven of these successfully made the one-mile flight, 4 of them coming in on the first night and 3 on the second. The first ones arrived in 8, 25, 32 and 82 minutes; those on the following night arrived at 1:10, 4 and 4:10 a. m. It is interesting to note that it was possible for one moth to make the flight of a mile in 8 minutes; in fact, he got home before I did, and my son had him caught and properly recorded when I arrived. And this moth had never been out of doors before and was only one day old when liberated!

Exp. 32. May 26. Wind, east; station, 1 mile west. This test was precisely the same as the last, excepting that wild males which had flown to the laboratory only that morning at dawn were used. They were 15 in number, and were liberated at 11:45 p. m. Five returned at the following times: 12:03, 1:12, 1:22, 1:55 and 2 a. m. Thus the sprightliest of these made almost as good time as a human competitor.

In the preceding four experiments it is evident that some of the male cecropias came in at hours that differ greatly from their regular hour of dawn. These were undoubtedly influenced by the light of the moon, but an analysis of the data in a later chapter shows that the bred males are more subject to this influence than the native ones.

Exp. 33. May 27. During the dawn, in addition to the marked cecropias which returned, 58 wild ones came in, of which 47 appeared young and 11 old.

Exp. 34. May 27. Wind, east; station, 1¾ miles west. Twelve unmated bred males, from 26 to 30 hours old, were liberated in or near the path of the wind, at 10:50 p. m. Two came in that night at 12:01 and 12:18 a. m., one each at dawn of the third day and fourth day thereafter. The first two made the distance of 1¾ miles in the brief time of 1⅓ and 1⅔ hours.

Exp. 35. May 27. Wind, east; station, 1¾ miles west. All conditions were the same as the last, excepting that experienced fliers were used; these 11 cecropias had all made one test flight before. Three of these returned that night, the first at 12:50, having made the trip in two hours, and the other two at dawn. Here the experienced fliers did no better than the novices.

Exp. 36. May 27. Wind, east; station, ½ mile east. Four

bred cecropias, from 1 to 4 days old, were liberated at 11 p. m., where the wind blew from them toward the females. To my suprise, one, four days old, came back at 12:37.

Exp. 37. May 27. Wind, east; station, 1 mile east. In this test 19 wild males which had flown to the roof that morning, and 2 which had returned in a previous test, were liberated in an unfavorable wind at 11:05 p. m. Two returned the following dawn, one on the second and one on the third morning later. The first three were young, and the last one to return was old.

Since this was a test to see if the males can fly to the females when the wind is not favorable to carry odors to them, we really should consider only those which came in the first night before the winds shifted. I do not want to juggle my evidence, but may it not be that mere chance might lead 2 out of 21, through aimless wanderings, into the path or region of the attraction?

Exp. 38. May 27. Wind, east; station, 1½ miles east. Ten young and 4 old wild males which had come in that morning, and 4 which had made two other flights, were taken out at 11:10 p. m. for this long flight in an unfavorable wind. Just one returned, making the mile and a half in two hours.

Exp. 39. During the dawn of May 28, 19 native cecropias flew in, of which 10 were old and 9 young. Were these morning visitors fewer because the wild population was becoming depleted, or because females other than ours existed and were diverting the attention of the wild males or perhaps our experimental moths as well?

Exp. 40. May 28. Wind, southeast; station, 3 miles northwest. This daring experiment was tried with a large number of males of various histories, to see if it is possible for the moths to return for a distance of three miles when the wind is in their favor, that is, blowing from the females toward them. There were 28 bred males one and two days old, 12 bred males which had made successful previous flights, 17 wild ones which had come in at dawn that morning, and 22 from the morning before, making a total of 79 moths. Only one returned, and that on the morning of June 1, so it seems to have come in by chance, although it is interesting to learn that they wander as far as three miles in their quest. I feel confident that these creatures are capable of returning that distance directly, instead of by

chance, if the direction of the winds could be exactly ascertained and urban hindrances eliminated.

Exp. 41. May 28. Before midnight a heavy fog settled over the landscape and the wind ceased; there was not enough breeze to flutter a leaf or waver a film of light smoke in the air. No moths appeared until the hour of dawn, when 28 came in (27 young native males and one marked bred moth) in spite of the presence of the fog and the lack of wind.

Exp. 42. May 29. For the first half of the night the moon shone brightly; after midnight it was partly obscured by clouds; a fitful wind blew from the east. Although several fine young females were on the roof, no cecropias came in until 3:40 a. m., when 8 young strangers and one marked one which had been liberated one mile east three days before, came in. Since they were so few, there was ample time for me to watch their arrival; most of them came from the west or the southwest. Some of them missed their mark and flew too far, over the housetop, but returned after a few moments. The dearth of males was conspicuous, but on second thought it was not surprising. During the first few experiments there was a dearth of females from my cocoons in the laboratory, but at this time the majority of those emerging were females, and the shortage was among the males. If this condition was duplicated in the wild population, it is easy to see how the few wild males would be abundantly occupied in their native haunts. May it be, also, that the gentle summer breezes did not carry the emanations of the females as far as did the strong, direct winds of a few days before, and hence reached only those near by?

Exp. 43. May 30. Wind, faint breeze from east; station ⅓ mile east. The following 30 cecropias were liberated in Tower Grove Park at 9 p. m.: 7 natives that had come in at dawn of that day, 12 from the dawn before, 5 from two mornings before, four bred males aged one and two days, and 2 natives which had come in from a previous test flight. None of the bred cecropias returned, but at 11 p. m. one wild one which had come in the day before arrived, and at dawn three more wild ones returned, and the following dawn three more. This shows at least that four out of 30 (considering only those which came in the first night) could find the females against the odds of a dis-

advantageous wind for a distance of ⅓ mile, but, it must be remembered, those which returned had made a previous flight to the roof.

Exp. 44. May 30. The above paragraph tells the activities of moths under experimentation on May 30. Here we record the action of wild ones in their relation to the moonlight on the same night. The moon shone from 9 p. m. With an abundance of females of both cecropia and polyphemus on hand, males of both species were coming to the roof that night. In addition to the one marked cecropia recorded above which came in at 11 o'clock that night, 4 more wild ones came in at 11:35, 12:02, 1:50 and 3:10, and during the usual hour 10 more arrived. Thus in spite of the fact that the moths are attuned to fly at the hour of dawn, one third of these came in during the moonlight, contrary to the custom of the great majority. Was this because the moonlight was of just the right degree of intensity to simulate the dawn and elicit their response, or were these four individuals peculiarly endowed with some faculties for seeking their mates in any light, which their brothers did not share?

Exp. 45. June 1. I overslept, so made no records of the small hours of the night, but at 4 o'clock, when I arrived, 6 wild males were flying about the cages, and 9 more came in before 4:30, making a total catch of 15 this night.

Exp. 46. June 1. Wind, southeast; station, 2 miles north. Thirty-eight bred males, from 3 to 5 days old, were liberated in Forest Park, a little to one side of the path of the wind, at 4:45 p. m. These moths had never before been out of doors. Only one of this large number returned, and that at 10:30 the same evening, after an absence of six hours, for the trip of two miles, at an hour when most moths are at rest.

Exp. 47. June 1. Wind, southeast; station, 3 miles northwest. The point of liberation was chosen, as nearly as we could estimate, in the path of the wind. The 61 cecropias were: 12 native moths which had come in at dawn, 10 from the day before, 7 native moths which had made an additional test flight, 31 which had emerged in the laboratory the day before, and 1 bred male 4 days old. Of these 61 cecropias, 15, or about 25 per cent, returned from their enforced flight of three miles!

These returns are interesting in point of time and proportion

of moths of various histories. Of the 12 wild ones caught that morning, 4 returned (33 per cent); one came in the following dawn, 6 hours after liberation, one the morning of June 3, and two at dawn of June 4. However, only one came in at once, and the others wandered for two or three nights. Of the 10 caught the day before, 3 came in (also 30 per cent), but none the first night, two the second and one the third dawn. Of the 7 moths which had already flown to the roof twice (once voluntarily and once under test), just one returned, an hour and forty minutes after being set free at 10 p. m. Of the 31 bred males, one day old, 6 (near 20 per cent) came back, and, the more surprising, all the first night; the first ones came in at 10:50, 11:40, and 11:45, and the other three at dawn. This appears to be the most remarkable record yet established; for it is truly wonderful that so many moths should come back promptly from a distance of three miles, when mates must have been abundant in the very park where they were liberated. And last, but not forgotten, is our one bred moth, four days old, which distinguished itself by coming back in two hours and three minutes, in spite of its youth and inexperience; it, too, made the three miles without waiting for the customary hour of dawn. This makes 4 of the 15 which came in before their customary hour of flight. It is highly interesting to note that *all* which came in during the early hours of the night returned during the first night; those which came on following nights all came at dawn. There must be a reason; were the meteorological conditions during the early hours of the night of June 1-2 more favorable than those of the two nights following, or were these particular creatures which came in early endowed with finer sensitiveness or superior ability which enabled them to surpass their fellows, and would likewise have brought them in under different or even adverse conditions? And the splendid returns for the entire lot, 15 out of 61, elicit the same questions; just why should so many succeed in this severe test, when so many failed even in simple flights?

Exp. 48. June 1. During the night of June 1-2 the native males that flew in numbered 15; of these, 12 came at the usual hour, about dawn, and the other three came at 10:40, 11:50 and 1:35 o'clock. In addition, 8 marked cecropias, which have been

recorded in other experiments, came in. There was hazy moonlight before midnight, and 7 moths came in during that time. All of these came from the northward; the wind was from the south.

Exp. 49. June 3. The moon was hidden during the early hours of the night of June 2-3, but at 3 a. m., when I took my position on the roof, a half moon was shining. The first male arrived at 3:27 and the last at 4:25. There was a very slight breeze from the south, sometimes shifting to the southeast; all of the moths came from a northerly direction. There were 7 young native moths and 5 marked ones already accounted for elsewhere.

Exp. 50. June 4. The early hours of the night had been very dark; when I took my post on the roof at 3 a. m., a half moon was shining and the wind was blowing from the southeast. The first male flew in at 3:35, and the last one at 4:30. Only 6 native and two marked moths flew to the cages during this period.

Exp. 51. June 4. Wind, south; station, ½ mile north. The 65 males used in this experiment had accumulated from the following sources: 9 wild moths had come to the roof two days before; 18 wild moths had come to the roof one day before; 7 wild males had come in at dawn that morning; 14 bred males had emerged from their cocoons three days before; 8 bred males had emerged that day; 9 bred males, two and three days old, had already mated. These were liberated ½ mile away, as nearly as possible in the path of the wind, at 9:45 p. m.

Of the first lot, only 1 of the 9 returned, and he came in at dawn, after an absence of six hours. Of the next lot of wild ones, 5 out of 18 came in, two of them in 35 and 65 minutes and the other three at dawn. The younger wild males distinguished themselves by making the best record; 4 of the 7 came back, one at 1:07 a. m., and the others at dawn. Whether this superior ability is to be explained by the probable youth of the contestants, or by the fact that they had more recently made the flight to the roof (when they had come in of their own volition), and thus, in some way, profited by the experience, we shall not here presume to decide, but only take cognizance of the fact that this is the second time this condition has occurred, where, in

exactly parallel tests, the wild males which had flown to the roof at dawn of the same day were conspicuously more successful than their brothers who had come in similarly one or two days before. Out of 14 bred males, three days old, 4 returned; none of these waited for dawn, but all arrived between 12:15 and 1:20 a. m. Of the 8 moths which had emerged the same day, two returned the same night at 11:40 and 1:20 o'clock, and two more came in two nights later. In the last lot of mated males, 2 out of 9 returned the same night at 11:20 and 12:50. This shows, again, that even after having mated, the moths respond to the attraction of the females for a distance of at least half a mile. Thus, out of the total of 65 that were liberated, 20, or 31 per cent, returned; 18 of these came the first night and 2 later.

Exp. 52. June 4. In addition to the marked moths that came in as recorded in the last experiment, during the night of June 4-5, 9 new wild males flew in. They did not wait, this time, for the usual hour of flight, but they were well distributed throughout the night, from 10:30 until dawn. The cecropia season was drawing to a close. From our cocoons in the laboratory, only 22 emerged from June 5 to 8, and none at all after that.

Exp. 53. June 6. During the hour of dawn, 7 wild moths and 1 marked one (already accounted for) came in from the north. The breeze was from the south.

Exp. 54. June 7. Being badly in need of sleep, I did not get up during the night to receive the eager lovers, but at 7 a. m. I found 6 wild cecropias (4 old and 2 young) at the cages.

Exp. 55. June 9. Wind, northeast; station, ⅛ mile south. Several cages full of cecropia females, two and three days old, were exposed to the gentle breeze on the roof. Three males, each with one-half of each antenna removed, were liberated at 9:14 p. m., ⅛ mile south, a little to one side of the path of the wind. At the following dawn, one of these came back.

Exp. 56. June 10. During the customary hour of flight, 25 wild cecropias came in. All of these males were young. This large number, at the end of the season, would indicate that native females are scarce or too old to be attractive.

Exp. 57. June 11. The rain of the previous day continued,

with a strong wind from the east. Up to 3:40, no moths came in, and I fell asleep. At 7 o'clock I found that the lid had blown off one cage, and every one of the five females therein had united with a wild cecropia. This 100 per cent record of mating is more interesting when compared with the results of later experiments, wherein only 9 out of 28 couples mated when thrown in close proximity in small cages, but where all motion of the air was excluded. Six other wild males were found in the room.

Exp. 58. June 12. Wind, west; station, 1/5 mile east. The 22 native males were liberated at 11:15 p. m., in the park. These had come in during the last two dawns. The eyes of four of these were thickly painted with stove enamel; this was done to learn if the eyes do function in the moths' quest for mates. None of the normal males returned in this experiment, but, *mirabile dictu!* all four of the blinded ones came back that same night!

Exp. 59. June 12. Wind, west; station, 1/5 mile east. This lot included 10 cecropias which had come to the roof at dawn that morning, and the one which had come back successfully with only one half of its antennae. The antennae of all of the others were entirely removed. It was at first very flattering to find that we got a 100 per cent failure to return when the antennae were entirely amputated, in contrast to a 100 per cent ability to return with eyes covered, but of course our evidence from the antennaeless moths is weakened by the fact that the able-bodied moths the same night failed, for some reason which we cannot fathom. However, these two experiments give us some inkling of the relative importance of antennae and eyes.

Exp. 60. June 12. I watched all the night of June 12-13, but no cecropias came in during the early hours. Before midnight, the wind blew from the west, but at 3:20 it shifted to the northwest and became stronger. The first one came in at 3:25, and until 4:20, 26 young wild males arrived, and the four blinded ones mentioned above. This flock came in from the south and southeast. It is surprising to me that so many should come in at this date, inasmuch as the last of my cocoons in the laboratory had hatched four days prior to this. May it be that the shifting of the wind carried the emanations from the laboratory

over certain fields which for a few days had not been in the path of our breezes?

Exp. 61. June 13. While I was on the roof all night waiting for cynthias which did not return, I had leisure to watch for the arrival of cecropias also. This was a bright starlit night; the breeze was not perceptible, but the smoke issuing from a tall chimney rose high in the air and disseminated toward the southeast. My vigil was in vain, for none came early. During the dawn hour, 19 came in, 16 of which were from the southeast; the direction of the others was not noticed.

Exp. 62. June 15. Wind, imperceptible; station, 100 feet west. Fifteen wild moths which had come in at dawn on June 13, and 3 of the blind ones which had returned in Exp. 58, were used in this test: The eyes of all were covered with the black enamel. They were liberated 100 feet west, with no wind, at 11:30. At dawn, 3 of these came in; those which were out for their second sightless flight were not among them.

Exp. 63. June 15. Wind, none; station, 100 feet west. Fifteen moths with mutilated antennae figured in this test. Five of these had half of each antenna off; five were without the entire left antenna and five without the right; two normal moths were added as controls. During the following dawn, 4 of the mutilated cecropias (two with half of each antenna, one with right and one with left antenna) returned, but only one of the normal moths came back, and he came only as a wanderer a day later. I wanted to repeat this test with a large number of moths, to see if, as appears here, those with half of each antenna are more capable of following a trail than those with all of only one antenna, but the quantity of material was too depleted to afford them in large numbers.

Exp. 64. June 16. While I was kept busy all night catching cynthia males which came to the roof, no cecropias came before 3:40, and they ceased at 4:25. During that 45 minutes, 15 wild and 7 marked cecropias came in. It was suprising that among the 15 wild ones, all but 2 appeared young, perhaps a day old; this indicates that the Missouri wild moths were emerging later than my New York stock.

Exp. 65. June 17. I waited all night and took the cynthias which came in. The work so far indicates that these

two sister species have quite different habits. The cecropias concentrate their activity about and just before the hour of dawn, and only occasionally some aberrant or strangely stimulated individuals fare forth during the earlier hours of the night. The cynthias, on the other hand, prefer the midnight hour for their flight, and seldom are caught abroad at dawn. And so this night the first cecropia came in at 3:40 and the last at 4:25, 12 native males and 1 blind moth from an earlier test.

Only a few decrepit old female cecropias remained on the roof; it seemed unlikely that these could retain their powers of attraction. In fact, on this night and the preceding one, it was apparent that the incoming males showed an unusual amount of indecision in settling on the cages; they flew about aimlessly before they came near the cage, and even then they would sometimes fly away without stopping. Out of the 13 male cecropias, only one eventually settled on a female cecropia's cage, while 6 settled on cages of young cynthias, and the remainder were captured with the net when I thought they were about to escape. It is interesting to note here that, while the cynthias were of various ages from one to six days, one cecropia alighted on the cage containing the day-old cynthia and 5 cecropias chose the two-day old cynthias and ignored the others.

Exp. 66. June 17. Wind, east;; station, ⅕ mile west. The previous experiment gave evidence that the male cecropias are to some extent attracted by cynthia females. I now had in my possession two old and decrepit cecropia females. These were taken to the rooms below and locked up in an almost air-tight closet. Then with plenty of young cynthias on the roof, at 11:50 p. m. I liberated 30 male cecropias in the path of the wind, as nearly as I could estimate, and ⅕ mile distant. The lot included 2 males which had returned minus half of each antenna, 2 which had returned with blackened eyes, 11 wild males had come in at dawn that morning, and 15 from dawn of the day before. None of these 30 returned, but 8 young wild cecropias flew in on the roof.

Exp. 67. June 18. Wind, south; station, 200 feet north. Wishing to test again the reaction of cecropia males to cynthia females, I took all the males I had, 14 in number, and liberated them in the direct breeze. Eleven of these had been fooled once

by the cynthias, and the other three, twice. Perhaps they had been misled too often, for none came to the roof again; but the attraction was potent to the inexperienced young males, due either to their unsophistication or their youthful antennae, for at dawn 14 new wild male cecropias came in, when we had not a cecropia female on the place! But let us give them credit for the fine discrimination which they exhibited, for they were extremely active in their flight and not one actually alighted on the cages, but fluttered about for some minutes as if in confusion, and then wandered away. Only when they were escaping thus were they captured with the net. It should be emphatically stated that this indicates a certain kinship between the two species. It denotes, in my opinion, that the parting of the ways of the two species has been comparatively recent; that the cecropias have not travelled far enough from cynthias, phylogenetically speaking, to have altogether lost the recognition of the familiar odor.

Exp. 68. June 20. I was up all night and captured about 70 cynthias, but no cecropias came before 3:20; then only 5 came in. These came, of course, in response to the cynthias' lure, since all cecropia females had long since ceased to exist.

Exp. 69. June 25. The last wild cecropia flew to the cynthia cage on the roof at 4 o'clock this morning.

Summary.

In reviewing the experimental work on cecropias, we find that when the females are placed in cages at the open windows or on the roof, the wild males and also those bred in confinement and liberated at various distances come to the cages durin the night. During the period of experimentation, May 7 to June 25, 961 males flew to the cages on the roof. Of this number, 170 were marked moths which had been bred from New York cocoons and had been liberated at various points and directions in an attempt to learn what distance they can travel and what factors determine their guidance. During this period, 791 native wild males flew to these cages containing the New York females. Of course no females came in, and none were taken out on test flights. The age of these wild moths can be approximately estimated by the condition of the wings. Of those which came in, 715 were obviously fresh, young ones, and 76 appeared old and tattered.

I have said that these insects were attracted by the female cecropias; this statement needs to be amended somewhat, for in the last four experiments, 28 male cecropias came to the cages containing only the cynthia females, after the cecropia females were all dead; they were deceived by the similar or related cynthia emanations. The behavior of the cecropia males showed, however, that the deception was not complete.

A summary of the data shows (see Table No. 1), that out of 735 marked males liberated in various directions and at distances varying from 25 feet to 3 miles, 170 returned to the females on the roof. This was 23.1 per cent of those liberated. If this result seems small to the reader, let me remind him that in the region where 791 wild males came to us voluntarily, there must have been an enormous number of females in the open to entice our experimental moths from their path; hence to me it seems really wonderful that any at all should return to a bleak, second-story roof in an area of roofs and brick walls. The percentage of returns of this species, a native of Missouri, compares well with the returns of the cynthias, which had the field completely to themselves, since in the wilds of this city there are no females of his species to waft her emanations on the breezes and thus swerve him from his course. Later pages will show that the per cent of returns of cynthia was 31. In the light of this comparison, I feel doubly assured that the returns of cecropia are good.

A tabulation of the figures shows that the 170 which were liberated at various times during the evening came in during the dawn* of the first, second, third and fourth morning in the following proportion:

1st morning, 106.
2nd morning, 50.
3rd morning, 11.
4th morning, 3.

The time of flight is defined with surprising sharpness; it seems to be the established habit of this species to make the nuptial flight during one hour, just before and during the period of dawn, from 3:30 to 4:30 o'clock, with deviations from this time seldom exceeding five or ten minutes, excepting in the cases mentioned in the footnote.

*In a few experiments the moonlight elicited an earlier response.

TABLE No. 1
SAMIA CECROPIA

Experiment	Date	M—Mated U—Unmated W—Wild	Weather	Time of Liberation	Wind From	Wind Favorable	Distance from Home Miles	Direction from Home Liberated	Number Liberated	Number Out for First Time	Number that Made Previous Trips	Age of Males (bred) Days	Returns					First Timers		Experienced Fliers		Strays	
													First Day	Second Day	Third Day	Fourth Day	Total Returns	No. Liberated	No. Returned	No. Liberated	No. Returned	Old	Young
1	May 7	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
2	7	2 W 1 U	After Shower	6:30 p.m.	S. W.	Yes	⅛	E	3	1	2	1	1	.....	.....	.....	1	1	1	2	0	.....	.....
3	7	1 U	After Shower	8:05 p.m.	S. W.	No	⅛	W	1	0	1	1	.....	.....	.....	.....	0	0	0	1	0	.....	.....
4	7	M	After Shower	9:00 p.m.	S. W.	Yes	⅛	E	1	1	0	2	1	.....	.....	.....	1	1	1	0	0	.....	.....
5	7	M	After Shower	10:15 p.m.	S. W.	Yes	½	E	1	0	1	2	1	.....	.....	.....	1	0	0	1	1	.....	.....
6	7	M	After Shower	11:50 p.m.	S. W.	Yes	1⅛	E	1	0	1	2	.....	.....	.....	.....	0	0	0	1	0	.....	.....
7	14	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
8	15	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	7
9	16	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	12
10	17	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0
11	17	2 W 2 U	Shower	6:30 p.m.	S	No	⅛	E	4	2	2	6 days 4½ hrs.	.....	.....	1	.....	1	2	1	2	0	.....	2 .....
12	18	.....	Rain	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
13	18	23 W 1 M	.....	9:00 p.m.	S. E.	Yes	1	N. W.	24	0	24	.....	1	3	.....	.....	4	0	0	24	4	3	39
14	19	W	.....	10:00 p.m.	S	Yes	½	N	53	0	53	.....	5	9	1	1	16	0	0	53	16	.....	‡53
15	20	6 U 33 W	.....	10:30 p.m.	None	No Wind	½	E	39	0	39	.....	4	10	.....	.....	14	0	0	39	14	.....	‡33
16	21	36 W	.....	7:30 p.m.	N. E.	Partly	½	S	36	0	36	.....	4	2	3	.....	9	0	0	36	9	.....	‡89
17	21	W	.....	7:25 p.m.	N. E.	Partly	1	S	36	0	36	.....	2	.....	1	.....	3	0	0	36	3	.....	.....
18	21	U	.....	7:30 p.m.	N. E.	Partly	½	S	8	7	1	1 & 2	1	.....	.....	.....	1	7	0	1	1	.....	.....
19	21	.....	.....	7:30 p.m.	N. E.	Partly	½	S	11	0	11	.....	5	.....	.....	.....	5	0	0	11	5	.....	.....
20	22	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
21	22	44 W 6 U	.....	.....	N. E.	Yes	2	S. W.	50	6	44	1 to 3	.....	1	1	.....	2	6	0	44	2	.....	113 .....

*22	23																							
24	23	W		8:00 p.m.	E	Yes	1/100	W	27	0	27			10			10	0	0	27	10		
25	24								23	0	23		11				11	0	0	23	11		
26	24	W		11:50 p.m.	E	Yes	1/200	W														23	25
27	25								5	0	5		3				3	0	0	5	3		
28	26		Rain																			15	26
29	26		Moon	11:55 p.m.	E	Yes	1/200	W	14	0	14		5	1			6	0	0	14	6		20
30	26		Moon	11:58 p.m.	E	Yes	⅛	W	31	0	31		12	1			13	0	0	31	13		
31	26	U	Moon	11:48 p.m.	E	Yes	1	W	13	13	0	1 to 3 days	4	3			7	13	7	0	0		
32	26	W	Moon	11:45 p.m.	E	Yes	1	W	15	0	15		5				5	0	0	15	5		
33	27																					11	47
34	27	U		10:50 p.m.	E	Yes	1¾	W	12	12	0	1	2		1	1	4	12	4	0	0		
35	27	W		10:50 p.m.	E	Yes	1¾	W	11	0	11		3				3	0	0	11	3		
36	27	U		11:00 p.m.	E	No	½	E	4	4	0	1 to 4	1				1	4	1	0	0		
37	27	W		11:05 p.m.	E	No	1	E	21	0	21		2	1	1		4	0	0	21	4		
38	27	W		11:10 p.m.	E	No	1½	E	18	0	18		1				1	0	0	18	1		
39	28																					10	9
40	28	U W		9:45 p.m.	S. E.	Yes	3	N. W.	79	28	51	2				1	1	28	0	51	1		
41	28																						28
42	29																						8
43	30	W U		9:00 p.m.	E	No	⅛	E	30	3	27	1 to 2	4	3			7	3	0	27	7		
44	30																						14
	June																						
45	1																						15
46	1	U		4:55 p.m.	S. E.	Yes	2	N	38	38	0	3 to 5	1				1	38	1	0	0		
47	1	W U		10:00 p.m.	S	Yes	3	N	61	32	29	2 & 4	9	4	2		15	32	6	29	9		
48	1																						15
49	3																						7
50	4	W U																					6
51	4	W U		9:45 p.m.	S	Yes	½	N	65	31	34	1 to 4	18	2			20	31	10	34	10		
52	4																						9
53	6																					7	
54	7																					4	2
56	10																						25
57	11																						11
60	12																						26
61	13																						19
64	16																					2	13
65	17																					1	11
66	17																						† 8
67	19																						†14
68	20																						† 5
69	25																						† 1
Tot.									735				106	50	11	3	170	178	32	557	138	76	715

‡Dawn following. †–Cecropias are all dead. The males flew to Cynthias. *Indoor experiment.

In considering the return of the moths when liberated in favorable or unfavorable winds, only the 106 which came in during the following dawn may really be accepted as reliable evidence, since we cannot know what factors, the shifting of winds, the interference of other mates, etc., are responsible for their wanderings. Even when only a few hours elapse between the time of liberation and the hour of return, there is abundant chance for the wind to change for a time, or to be deflected by the obstructions of the city. Out of 630 moths set free in favorable or partly favorable winds, or no wind, 98, or 16 per cent, returned at the following dawn; out of 78 liberated in a wind which was at the time of liberation unfavorable, 8, or 10 per cent, returned. This method of studying the direction of flight of the moths and their method of orienting themselves in relation to the wind is not so fruitful of results as merely to watch keenly in the moonlight or dawn, and see from what direction they fly. At times the moths came too thick and fast for me to see their direction, but in the many cases where I was able to make this observation, the great majority of them arrived flying against the breeze. In the experiments with cynthias, as you will see later, we found data much more conclusive in favor of their coming home against the wind; here we find that with the wind favorable for carrying the female odor to the point of liberation of the males, 38 per cent returned, and in an unfavorable wind only 8 per cent returned. This type of experimentation and deduction is the correct one for cynthia, for these moths fly early in the night; this is so soon after the time of liberation that there is little chance for the change of wind. Moreover, their attention is not diverted by wild females in the shrubbery.

Thus the majority of them came galloping in facing the wind, from which we conclude the wind had carried them the message of the whereabouts or at least the direction of their mates. Some proved their ability to come in repeatedly, and some of these distinguished themselves either for speed or for overcoming difficulties. Whether this superior ability was due to finer native sensitiveness, which resulted in superior ability in this most vital quest, or whether their native endowment was augmented, after one or two experiences (which covered a tenth or more of their natural lifetime), by associative memory which

aided in their later returns, I shall not presume to say at this point. I should like to think that these creatures profit by experience, but in a purely speculative way it seems more logical to attribute this superior ability to the natural (sensory) endowment of certain individuals. In their natural wild life, generation after generation, these moths have no possible use for the ability to remember the trysting-place with their beloved and return to it, but it is hard to conceive of anything more vital in the perpetuation of the species than a fine native sensitiveness whereby the male can once locate his distant and unseen mate. The more specialized this sensitiveness, the greater chance the individual has of leaving like progeny, for certainly the male that is lacking or deficient in this native faculty is in no danger of perpetuating his stupidity.

Basing my judgment upon the action of the great majority of these moths observed, I feel convinced that the medium of attraction between the sexes is odor, or *something so closely akin to it that we need not seek another name for it;* that the males follow this odor trail on the wind to the site of the female, and that they cannot orient themselves toward the female until they come by chance into a current of air carrying her emanations.

When we tabulate the ratio of returns to the distance which the males had to travel, we get the following results:

Experiment No.	Number Liberated	Distance Miles	Number Returned	Per cent Returned
26, 29	19	1/200	9	47
24	23	1/100	11	48
2, 3, 4, 11, 30	40	1/8	16	40
43	30	1/3	7	23
5, 14, 15, 16, 18, 19, 36, 51	217	1/2	67	31
13, 17, 31, 32, 37	109	1	23	21
6	1	1 1/6	0	0
38	18	1 1/2	1	5
34, 35	23	1 3/4	7	30
21, 46	88	2	3	3
40, 47	140	3	16	11
Total	708		160	

Too many factors are complicated in these data to throw much light on the distance traveled and the per cent that returned. It would be interesting indeed if all the interfering factors could be eliminated, such as distraction of wild moths, shifting winds, etc., and a pure test could be made of the distance from which they are capable of detecting and discovering their mates. Surely everyone will agree that the return of 16 marked moths, or more than 10 per cent of those liberated in this test, from a distance of three miles is truly marvellous. Since this was accomplished amid the aforementioned conflicting factors, it is logical to believe that their ability *per se* to pick up and follow a trail would far exceed this surprising distance.

The table reveals the fact also that the experienced males, i. e., those which have made one or more successful flights to the roof, came back in a larger per cent of cases than did those out for their first flight. In 178 cases of the males taken out for the first time, 32, or 18 per cent, returned; in 557 records of males taken out that had previously flown to the roof one or more times, we got a return of 138, or nearly 25 per cent. This compares well with the results from cynthias, described elsewhere in these pages, in which we get returns for inexperienced and experienced fliers of 30⅓ and 37 respectively. In both species the difference between the two classes is 7 per cent.

The hour of activity of the cecropias was always (excepting a few cases during bright moonlight or abnormal temperature) between 3:30 and 4:30 a. m. Even when the moths were liberated no further distant than our own back yard, and either early in the night or at 2:30 a. m., they showed no inclination to come in until 3:30, probably when the light stimulus began its work. At first thought the reader might suspect that the hour of dawn would vary considerably during the long period of experimentation, but while this would be true for any other time earlier or later in the summer, the hour of dawn just before and after the summer solstice is more nearly constant than at any other time during the summer.

In summarizing the work on cecropias, we must not overlook the evidence gleaned from the behavior of moths deprived of the use of their eyes and antennae. We find blind males flying to the females quite as readily as those with eyes uncovered.

TABLE No. 2

SAMIA SECROPIA (MUTILATED)

Experiment	Date, June	W—Wild U—Unmated	Time of Liberation	Wind From	Wind Favorable	Distance From Home, Miles	Directions from Home When Liberated	Number Liberated	Number Out First Time	Number That Made Previous Trips	Mutilation	Returns		
												First Day	Second Day	Total
55	10	U	9:14 p.m.	N.E.	Yes	⅛	S	3	3	0	½ of each antennae off	1	....	1
58*	12	W	11:15 p.m.	W	Yes	1/5	E.	22	....	22	4 eyes Blk. 18 normal	4	....	4
59	12	W.	11:15 p.m.	W.	Yes	1/5	E.	11	0	11	Both antennae completely off	0	....	0
62	15	W.	11:30 p.m.	No	Wind	1/50	W.	18	0	18	Blind.....	3	....	3
63***	15	....	11:30 p.m.	No	Wind	1/50	W.	17	....	....	2 normal; 5 half of each antennae off; 5 right off; 5 left off.	4	1	5
66**	17	W.	11:00 p.m.	E.	Yes	1/5	W.	4	0	4	.....	0	....	0
67**	18	W.	10:50 p.m.	S.	Yes	1/25	N.	14	0	14	.....	....	....	....

**There were no female Cecropias present, only Cynthias.
*Normal ones did not return but blind ones did.
***Returns—1 normal; 1 with right off; 1 with left off; 2 with half of each off.

In proof of their delicate sensitiveness, they came in response to the attraction of cynthia females after all cecropias were dead. We find the male cecropias flying home with one half of each antenna off, and to a slightly less degree with all of one antenna amputated, but none at all returned when both antennae were gone. See Table 2 above.

Experiments on *Platysamia cynthia.*

The cynthia moths began to emerge on May 14; the emergence was slow at the first of the season, only 8 individuals having appeared up to June 6. The period of emergence for the majority of the population seemed to date from June 7, so by June 10, sufficient material was on hand to make the first experiment. Since these moths are native of the Atlantic States, one may carry on work in St. Louis, in the study of long distance flights with the assurance that the marked males will not be attracted by females of their own species anywhere but in the cages on the roof. These moths, like the other species herein studied, have aborted mouth parts and require no food; this

eliminates the very difficult factor of proper nutrition of the organisms under experimentation. Enough factors remain, however, to be considered in these studies,—age of the moths, the effect of the wind, weather, fog, moonlight, starlight, lamplight, urban odors, etc. Through and under these modifying influences, we shall try to discover by what means these moths can orient themselves to their mates, and the extent of their abilities.

Exp. 1. June 10. Wind, faint breeze from northeast; light fog; station, ⅛ mile southwest. By 11:30 the breeze had become almost imperceptible and the fog was dense. A dozen female cynthias were displayed in wire cages on the roof. Eleven males, all 3 days old, were liberated at 9:14 slightly out of the path of the wind. Four of these returned at dawn.

Exp. 2. June 10. Weather same as above; station, ⅛ mile east. Eight young males were liberated at 9:35 p. m. Two of these flew to the roof at 3:00 and 3:55 a. m.; the first was found resting quietly on a cecropia cage and the other alighted on a cynthia cage.

Exp. 3. June 10. At 3 p. m., when I was painting numbers on the wings of the newly emerged moths, one escaped and flew out the window and away, high over the housetops. At 10:20 that night it came flying back to the cynthia cages as joyously as if it had not fled the spot a few hours before.

Exp. 4. June 12. Wind, slight, intermittent breeze from west; station, ½ mile east. The 7 males included 5 unmated ones ½ day old and 2 mated ones, 1 day old. They were liberated in the park at 11:10 p. m. Only one returned, a previously mated individual, at 12:20.

Exp. 5. June 12. Wind, same as Exp. 4; station, 1 mile east. For this experiment, we used the 7 moths which had already come back from the former test flights and 7 new ones, all one day old. All were set free in the park at 11 p. m. Only one returned out of these 14; it was 5 days old and had made a previous flight, and it made this flight of one mile in three hours. At first it was thought that possibly the experienced fliers were too old, but since the only one to return was one of the old ones, it seems that other factors must have entered into the problem.

Exp. 6. June 14. During the afternoon, two male cynthias escaped while being handled, and promptly fled; at 12:20 and 12:30 a. m. they came back.

Exp. 7. June 15. Wind, not perceptible; station, ⅛ mile west. Twenty male cynthias, all less than one day old, were liberated at 11:10 p. m. Just one half of these, or ten returned; nine came in between 11:20 p. m. and 1:40 a. m., and one at dawn. I have not yet discovered a reason why these should be so much more agile in returning than were their brothers in apparently comparable tests.

Exp. 8. June 15. Wind, imperceptible; station, 1 mile west. Eighteen unmated cynthia males, all two days old, were liberated. It is interesting to find that while in the last test 50 per cent returned from ⅛ mile west, here 22 per cent returned from one mile in the same direction under the same conditions. The four returned at 11:35, 1:15, 2:05 and 3:40, the first one making the mile in 29 minutes.

Exp. 9. June 15. Time, place and weather, same as Exp. 8. Five males that had already mated, four of them once and one of them twice, were also liberated one mile west, to see if mated males are less or more responsive to the lure. Only one returned, at 3:45. The numbers are too small to show anything excepting that the mated males appear in no way different, in ability or inclination, from the unmated individuals.

Exp. 10. June 15. Wind, imperceptible; station, ½ mile north. On the same night of the eminently successful experiments just preceding, we tried liberating moths in the other directions of the compass. Twenty-four males one-half day old were set free ½ mile north at 10:58. Only one returned that night, at 12:45; two more came in the following night.

Exp. 11. June 15. Wind, imperceptible; station, ½ mile east. These 22 young males, ½ to ¾ day old, were set free in the park east of the house at 11:25. While 4 eventually returned, only one came in the same night, at 1:40, and can be considered as really significant. Thus the returns from both of these last two directions were really negligable; in both experiments the individuals were out long enough to come upon the trail by aimless wandering.

Exp. 12. June 15. Wind, imperceptible; station, ½ mile south. Under exactly the same conditions, 22 males were liber-

ated ½ mile south. This lot consisted of 15 moths 1½ days old and 7 which were 2½ days old. None of the older moths returned, but 4 of the 1½ day old ones came back, and all the same night, at 12:30, 1:23, 1:41 and 3:40. Here the proportion, 18 per cent, would indicate that this direction held some condition imperceptible to us, which was more favorable to their return than the north or east, but less favorable than the west. Of course my secret suspicions were that a current of air moved gently toward the west or sometimes south.

Exp. 13. June 16. The foregoing experiments indicate that for some reason which I do not know the west is more favorable to the homecoming than any other direction. It seemed worth while to make one more attempt to solve this question. So at 1:55 a. m. of the night of June 15-16, I took stock of my male cynthias, and threw all of my available material into one more test. There were in all 32 individuals, 14 of which had just come in from tests, and 18 which had emerged within the last 24 hours. These were divided into two lots of 16 each and liberated in opposite directions, east and west, but at no great distance from the females. One lot, consisting of 7 young moths and 9 that had just come in from distant flights, was liberated 50 feet east of the house. Since the indication was that the west was more favorable to their return, I handicapped those taken west by giving that lot a preponderance of young males, and I gave those liberated at the east point an advantage by assigning to their lot a greater proportion of experienced fliers. Of the 16 liberated 50 feet east, only one came back that night (after one hour and a quarter), and another came in the following night at 10:55.

Exp. 14. June 16. Conditions same as above. The remaining 16 moths, consisting of 5 experienced fliers and 11 newly emerged males, were liberated 50 feet west of the house. Of these, 6 returned the same night and 4 the following night. It is interesting to note that, although their normal period of activity was broken in upon by our interference at 11:55 p. m., six of them extended their period of flight until from two to four o'clock, while those which laid over until the next night all performed at the hour of their own choosing, 10:55 to 12 p. m. May it be that these four merely considered that according to "union" rules it was already quitting time when they

were set free at five minutes before midnight and sat down without even trying to come in that night? It is surprising that out of the 5 experienced fliers, two returned, while of the very young ones 8 came in. It seems to me that this experiment shows clearly that the one direction is far more favorable for the return of the moths than the other; if it is not the motion of the air that creates this response from a certain direction, then what is it?

Exp. 15. June 17. Wind, southeast; station, 1½ miles northwest. Twenty-six cynthias, 6 of which were 1½ days old and 20 were less than one day old, were liberated near the path of the wind at a distance of 1½ miles, at 10:52 p. m. Only one returned, aged 1½ days, after a flight of 1⅔ hours.

Exp. 16. June 17. Wind, southwest; station, ¾ mile northwest. Nineteen males, less than one day old, were set free at 11 p. m. None of these returned. This lot was liberated in an ailanthus bush; this is the food plant of the caterpillars, and the insects upon emerging throw off the peculiar odor of this tree; hence it might be that the odor of this tree had something to do with diverting their attention or confusing them.

Exp. 17. June 17. Wind, southeast; station, 2¼ miles northwest. Twenty moths, 1½ days old, were liberated in Forest Park at 11:25 p. m. Two returned from this flight of 2¼ miles, one after only an hour and the other 4½ hours.

Exp. 18. June 17. Wind, southeast; station, 2 miles north. Twenty male cynthias, aged 1½ days, were taken to a point north, in Forest Park, at 11:35 p. m. One returned the same night, after 2 hours, and another did so the next night.

Exp. 19. June 17. Wind, southeast; station, 1/5 mile northwest. For this experiment, all the cynthia moths on hand were used. They were all held captive after having returned from previous flights, and their ages were as follows: 2 days old, 19; 3 days old, 2; 4 days old, 2; 17 days old, 2. These 25 were taken out a short distance, 1/5 mile, in the general direction toward which the wind was blowing, at 11:50 p. m. Eight of this lot returned, the first after only five minutes and the last after two hours and six minutes. All of these eight were two days old, but, of course, these predominated in the lot.

Exp. 20. June 20. Wind, southeast, station, 1½ mile west.

In the following group of five experiments, the male cynthias were liberated in the evening when the wind was blowing from the southeast and it continued in that direction until I returned at 4 a. m.; there was no moon. Twenty moths, half of which had emerged that day and half the day before, were set free at 9:30; none returned.

Exp. 21. June 20. Wind, southeast; station, ¾ mile northwest. Thirty-five male cynthias, ½ day old, were taken ¾ mile northwest at 9:55. Twelve of these eventually returned, but while all of them came in between the hours of 10:30 and 12:30, only one came in the first night (after 1½ hours); 9 came the second night, 1 the third, none the fourth, and one poor wing-sore creature straggled in at midnight the fifth night. This experiment begins to bring to the fore the factor of rhythmic periodicity, which is a fairly well established character in the activity of this species. Their habitual time of flight is between 10:30 and about midnight; if they do not reach their goal by the end of this period, on the first night, they lay over for the same hours the next night or even the next. All of these had the opportunity to come in at either an earlier or a later hour, but not one of the twelve in this experiment did so.

Exp. 22. June 20. Wind, southeast; station, ½ mile northwest. Thirty-eight male cynthias (20 one day old, and 18 two days) were set free at 10 p. m. Of these, 22 returned (11 from each lot) and, like the last ones, all came between 10:18 and midnight. All 22 came back the first night, or in less than 2½ hours after they had been liberated ½ mile from the cages of the females. I do not think the moths in this experiment came back more quickly because they were a quarter mile nearer home than those in the last test, but probably because they were liberated in a current of air more direct from the house. Just half of these came in during the first half-hour, 10 to 10:30.

Exp. 23. June 20. Wind, southwest; station, 1/5 mile east. The 38 males, aged 1½ days, comprised two lots, 20 which had never mated and 18 which had mated only a few hours previously. The purpose was two-fold: to get additional comparative data on the relation of distance to returns, and to ascertain if the mated or the unmated males respond more readily to the sex attraction. Of these 38, 20 returned, all but one, the same

night, and between 10:20 and 1:46. The first two came in in 10 and 12 minutes, and 8 arrived in the first hour. One came in at 11:53 the following night. In comparing the returns of the mated and unmated individuals, we find that of the 20 unmated one, 12 (60 per cent) returned, and of those previously mated, 9 (50 per cent) came back. This indicates that both are equally susceptible.

Exp. 24. June 20. Wind, southwest; station, 50 feet east. By 11 o'clock a number of moths had returned from their test flights and were available for another. Since I dared not venture far from the house on account of the constant arrival of others, I took these, 18 in number, and liberated them in the front yard, only 50 feet from the cages, and almost in the direction from which the wind came. This happened at 11:07 p. m., just in the time of the greatest activity of these moths. To my surprise, 11 returned, all the same night, but strange to say, in spite of the fact that they had only thrice the length of the room to travel, and they were set free at their most active period, only one made the tiny journey in less than an hour; the others required from 1¼ to 3½ hours to come in. Since 7 did not come back at all (please remember that the females in our cages were the only ones of this species in St. Louis), and since they consumed more time than did those which returned from half a mile, the same night, it seems possible that they fluttered aimlessly until, in time, they came upon the trail not far away. Of course, as an alternative, one may, if one chooses, evoke as an explanation for the return of the latter, the theory that these moths profited by their recent experiences in coming to the roof, and that place memory aided them in making the return once more. I offer no argument in favor of either theory.

Exp. 25. June 22. Wind, southeast; station, ½ mile south. The 27 moths used in this test included 10 less than one day old, which had already mated, and 17 from 1 to 1½ days old, which had not yet mated. These were liberated to one side of the direction from which the wind blew, at 9:50 p. m. None of these came back the first night, two of the mated moths returned the second night and one unmated one the third. Hence we must conclude that the ability of the moths to return under these conditions is negligible.

Exp. 26. June 22. Wind, southeast; station, ½ mile east.

These 21 male cynthias were unmated and from ½ to ¾ day old. They were liberated in Tower Grove Park at 10 p. m. The results were practically the same as in the last test, wherein the conditions were similar; none returned the first night, and two arrived about 11 o'clock the second night.

Exp. 27. June 22. Wind, southeast; station, north and slightly west, ½ mile. The 35 males were 1 to 1½ days old, and 21 of them had already mated. They were liberated at 10:08 p. m. in a large vacant lot ½ mile north, and a few rods west of the house. When I arrived home at 11 p. m., after attending to another experiment en route, I found the children in high excitement catching the moths; they had captured 12 which had arrived before I did, so I have not the exact time of their arrival; 7 more came in before midnight, and 2 more came at 12:40, making a total of 21 which returned with speed the first night; none came on later evenings. The deductions are self-evident. This series of four experiments, 25 to 28, shows clearly that when the moths are liberated in the path of the wind, many return promptly for a distance of ½ mile; if out of the path, they are lost. When we compare the flight of the mated and the unmated males, both of the same age, we find them practically equal; 64 per cent of the mated individuals came in and 57 per cent of the unmated ones.

Exp. 28. June 22. Wind, southwest; station, ½ mile west. These male cynthias, 22 in number, unmated, aged ½ to ¾ day, were set free at 10:35 p. m., to complete the series of tests from all directions being carried out this evening. For the third time we find that none came in the first night, 4 returned the second and 2 the third night, all during the usual period of flight of this species.

Could anyone imagine experiments to behave so obligingly—to warm the cockles of the heart of even an entomologist—as does this series! Of the 70 moths liberated in the three directions where the wind was unfavorable, not one returned that night, while of the 35 liberated near the path of the wind, 21, or exactly 60 per cent, came scurrying back, and more than half of them beat me home!

Exp. 29. June 22. Wind, southeast; station, 1 mile west. This test was the same as the last, excepting the distance was

doubled. The participants were 9 unmated cynthias, 1 or 1½ days old, and 12 which had made one or two previous flights. None of these ever returned. These five experiments, on the evening of June 22, wherein not one of the 91 moths liberated in an unfavorable wind returned that night, but a few came in later, somewhat justify our surmises in Exp. 24.

Exp. 30. June 24. Wind, southeast; station, 50 feet west. The activity of the moths so far has seemed to indicate that the period of flight for this species is about two or three hours before midnight. To test this, 36 male cynthias were liberated in the back yard at 8:10 p. m., with the wind almost favorable for their return. This lot included 6 moths ½ day old, 22 moths 1 day old, and 8 which had made a previous flight. Of these 36, 23 flew up to the cages on the roof; all but two did so before midnight, and those two came in only a few minutes later. None flew in immediately after having been liberated, although we know that they were fully capable of fifty times that distance if they would start at once. The first arrived at 9:16, over an hour after liberation, and the others followed thus: 9 to 10——8; 10 to 11—9; 11 to 12—4; 12 to 12:30—2. Since none at all came in before this period, although they had ample opportunity, and none after (I watched all night for more), we are safe in assuming that this is their chosen period of activity. By chosen, we mean chosen either by them or by circumstances, by the combination of stimuli to which they are attuned to respond. Since these stimuli or combinations of factors usually occur between these hours, the moths have the habit of staging their activities at this period, but if certain of the factors or stimuli to which they are attuned to respond are shifted to other hours, the moths change their program accordingly. But the point that is eternally puzzling to me is: *why* should the hour at dawn be the optimum time for the activity of cecropias, and two hours before midnight be likewise the optimum time for flight for these near relatives, whose other habits are very similar?

The proportion of returns in the various lots of moths is of only secondary interest in this experiment, but the data may as well be recorded for use elsewhere. Of the 6 moths, ½ day old, 2 came in; of the lot of 22 which were 1 day old, 16 returned. Of the 8 experienced fliers, 4 had made one flight and 4 had

made two flights previously. It is interesting that of those which had made one flight 1 returned, while of those which had made two flights, all four returned. This juicy morsel of data tempts one to rumination, but we had better refrain in this case, for this is probably only a matter of chance in dealing with small numbers. These five did not come in among the earliest, but just along with the others, from 9:35 to 11:07. Thus 33 per cent of the youngest moths came in, 77 per cent of those 1 day old, and 62 per cent of the old fliers. In all, 23 moths, or 64 per cent of the number liberated, returned; this is strikingly similar to the per cent (61) that returned from the front yard, the same distance in the windward direction. The chief difference lies in the fact that the latter were set free in the midst of their active period and still took a longer time to come in.

Exp. 31-31½. June 25. In the previous experiment we have seen that when male cynthias are liberated early in the evening they become active at about 9 o'clock, and the activity lasts until about midnight. In the cecropias, the similar period of activity is from 3:30 to 4:30 a. m. Experiments have shown that when cecropias are liberated early in the evening, they do not fly to the females, but wait for dawn.* Conversely, one would infer that if one liberated cynthias after their normal period of activity had ended, they would not fly to the females' cages that night, but would hold off flight until the following night, so they could fare forth at their usual hour. To put this question to test, the following cynthias were liberated in the early morning hours, after their normal period of activity had ended for that night: 6 males, 1½ days old, which were liberated at 2:45, and 18 that had come in before midnight, after having made two previous flights, which were set free at 3:15, in the back yard in a favorable location. Of the 6 young males liberated at 2:45, 3 returned, at 3:20, 3:24 and 3:27 a. m.; of the 18 experienced fliers, 11 returned between 3:22 and 4:15. This reveals at once that these moths do not postpone their flight until the next night, when liberated after their usual period of activity is past, but modify their habits and come in at some other time. In this they differ from the cecropias, who, for the most part,

*With very few exceptions.

stick doggedly to their usual program, excepting under unusual counter stimulation. But more than this is evident from this experiment. The first moths were liberated a half-hour before the second lot, yet they did not come in from the yard a minute sooner, but simultaneously with the latter. Now the dawn was just beginning to break at 3:20, and during the next ten minutes, the first 7 of these moths of both lots came in. May it be that, while the emanations of the females are the primary inducement to arouse the males to activity, yet a secondary stimulus may exist in light of a certain intensity, or meteorological conditions, or some such factor, to which also they are delicately attuned and to which they respond? In later experiments, recorded in the following pages, wherein tests were made within doors where conditions could be watched all the time, these moths showed, night after night, a periodic activity before nine o'clock, which brought all of the males to the window. This window, facing the street, admitted a subdued light from the street lamps, park lights and passing automobile lights. The full light of day streaming through this window did not elicit any response from the moths, but after a period of rest during the daytime and after nightfall, at about 8 o'clock, they presently flocked to the window. My opinion is that this mellow light from the various sources was very nearly akin to the light at break of dawn, and the moths react to both in the same way.

Exp. 32. June 27. Wind, southeast; station, 50 feet northwest. Previous experiments show that the male cynthias fly to the cages of their mates when the moon shines brightly. This test was now repeated, with the same wind and distance, 50 ft., on a dark night. 52 males were liberated in the back yard at 10:20 p. m. The moon was completely darkened by clouds. I harvested the returning moths until midnight, and since, by that time, I had sufficient data to show that he lack of moonlight is no deterrent to their activity, I went to bed. They began to come in a few minutes after their liberation, and up until midnight, 17 had arrived.

Summary.

Although tabulation loses much of the evidence yielded by the individual experiments, such a summary gives one a grasp of some aspects of the work as a whole.

TABLE No. 3
CYNTHIA MOTHS

Experiment	Date—June	M—Mated U—Unmated	Time of Liberation	Weather	Wind From	Wind Favorable	Liberated: Distance	Liberated: Direction From Home	Number Liberated	Number Out for First Time	Number That Had Made Previous Flights	Age of Males, Days	Returns: First Night	Returns: Second Night	Returns: Third Night	Returns: Fourth Night	Returns: Total	Number Returned First Flighters	Number Returned Experienced Flyers
1	10	U	9:14 p.m.	Fog	N. E.	Yes	⅛ Mile	S. W.	11	11	0	3	4	.....	.....	.....	4	4	.....
2	10	U	9:35 p.m.	Fog	N. E.	No	⅛ Mile	E	8	8	0	.....	2	.....	.....	.....	2	2	.....
3	10	U	3:00 p.m. Escaped	Fog	.....	.....	.....	.....	1	1	0	.....	1	.....	.....	.....	1	1	.....
4	12	5 U 2 M	11:10 p.m.	Slight Wind	W	Yes	½ Mile	E.	7	7	0	½–1	1 U	.....	.....	.....	1	1	.....
5	12	U	11:00 p.m.	Slight Wind	W.	Yes	1 Mile	E.	14	7	7	M2–5 U1	1 P	.....	.....	.....	1	.....	1
6	14	U	*2:30 p.m.	.....	.....	Yes	.....	.....	2	2	0	.....	2	.....	.....	.....	2	2	.....
7	15	U	11:10 p.m.	.....	No Wind	No Wind	⅛ Mile	W.	20	20	0	½–¾	10	.....	.....	.....	10	10	.....
8	15	U	11:05 p.m.	.....	No Wind	No Wind	1 Mile	W.	18	18	0	2	4	.....	.....	.....	4	4	.....
9	15	M	11:05 p.m.	.....	No Wind	No Wind	1 Mile	W.	5	5	0	.....	1	.....	.....	.....	1	1	.....
10	15	U.	10:58 p.m.	.....	No Wind	No Wind	½ Mile	N.	24	24	0	½	1	2	.....	.....	3	3	.....
11	15	U.	11:25 p.m.	.....	No Wind	No Wind	½ Mile	E.	22	22	0	½–¾	1	2	1	.....	4	4	.....
12	15	U	11:18 p.m.	.....	No Wind	No Wind	½ Mile	S.	22	22	0	1⅓–2½	4	.....	.....	.....	4	4	.....
13	16	U	1:55 a.m.	.....	No Wind	No Wind	50 Feet	E.	16	7	9	.....	1	1	.....	.....	12	2	.....
14	16	U	1:55 a.m.	.....	No Wind	No Wind	50 Feet	W.	16	11	5	.....	6	4	.....	.....		8	2
15	17	U	10:52 p.m.	.....	S. E.	Yes	1½ Mile	N. W.	26	26	0	6–1½ 20–⅔	1	.....	.....	.....	1	1	.....
16	17	U	11:00 p.m.	.....	S. E.	Yes	¾ Mile	N. W.	19	19	0	½–¾	.....	.....	.....	.....	0	0	.....
17	17	U	11:25 p.m.	.....	S. E	Yes	2¼ Mile	N. W.	20	20	0	1½	2	.....	.....	.....	2	2	.....
18	17	U	11:35 p.m.	.....	S. E	No	2 Mile	N.	20	20	0	1½	1	1	.....	.....	2	2	.....
19	17	U	11:50 p.m.	.....	S. E.	Yes	½ Mile	N. W.	25	0	25	See Exp.	8	.....	.....	.....	8	.....	8
20	20	U	9:30 p.m.	.....	S. E.	No	1½ Mile	W.	20	20	0	¾–1½	.....	.....	.....	.....	0	0	.....
21	20	U	9:55 p.m.	.....	S. E.	Yes	¾ Mile	N. W.	35	35	0	½	1	9	1	1	12	12	.....

22	20	U	10:00 p.m.	.....	S. E.	Yes	½ Mile	N. W.	38	38	0	1–2½	22	.....	.....	.....	22	22	.....
23	20	18 M 20 U	10:10 p.m.	.....	S. E.	Yes	1/6 Mile	N. W.	38	38	0	1¼–1¾	20	1	.....	.....	21	21	.....
24	20	U	11:07 p.m.	.....	S. E.	No	50 Feet	E.	18	0	18	.....	11	.....	.....	.....	11	.....	11
25	22	17 U 10 M	9:50 p.m.	.....	S. E.	No	½ Mile	S.	27	27	0	M¾–1 U1–1½	0	2	1	.....	3	3	.....
26	22	U	10:00 p.m.	.....	S. E.	No	½ Mile	E.	21	21	0	½–¾	0	2	.....	.....	2	2	.....
27	22	21 M 14 U	10:08 p.m.	.....	S. E.	Yes	½ Mile	N. W.	35	35	0	1–1½	21	.....	.....	.....	21	21	.....
28	22	U	10:35 p.m.	.....	S. E.	No	½ Mile	W.	22	22	0	½–¾	0	4	1	1	6	6	.....
29	22	U	10:30 p.m.	.....	S. E.	No	1 Mile	W.	21	9	12	1–1½	.....	.....	.....	.....	0	.....	.....
30	24	U	8:10 p.m.	Bright Moon	S. E.	Yes	50 Feet	N. W.	36	28	8	½–1	23	.....	.....	.....	23	18	5
31	25	U	2:45 a.m.	No Moon	S. E.	Yes	50 Feet	N. W.	6	6	0	1½	3	.....	.....	.....	3	3	.....
31½	25	U	3:15 a.m.	No Moon	S. E.	Yes	50 Feet	N. W.	18	0	18	.....	11	.....	.....	.....	11	.....	11
32	27	U	10:20 p.m.	Rain	S. E.	Yes	50 Feet	N. W.	52	52	0	1–3	17	.....	.....	.....	17	17	.....
Total.....	.....	.....	.....	.....	.....	.....	.....	.....	683	581	102	.....	180	.....	.....	.....	214	176	38

*About

It will be seen in Table 3 that in the 32 experiments, 683 male cynthias, which had emerged from their cocoons in the laboratory, were taken out in various directions and liberated at various distances, ranging from 50 feet to 2¼ miles. Out of this number, 214, or 31 per cent, made their way back to the females on the roof. Of these, 180 came in the first night.

Let us first summarize our data on the return of the moths in favorable or unfavorable winds—that is, winds which blow from the caged females toward the males, and those which do not. Exp. 16 is omitted from this summary for the reason given elsewhere and only those moths which came in the first night are considered, because the later ones were subject to varying winds which could not be traced.

Favorable Wind.

Liberated	Distance	Returned	Per Cent
128	50 feet	58	45
31	1/8 mile	14	45
63	1/5 mile	27	43
80	1/2 mile	44	55
35	3/4 mile	1	3
37	1 mile	6	16
26	1½ mile	1	4
20	2¼ mile	2	10
420		153	36

Unfavorable Wind.

Liberated	Distance	Returned	Per Cent
34	50 feet	12	35
8	⅛ mile	2	25
138	½ mile	6	4
21	1 mile	0	0
20	1½ mile	0	0
20	2 miles	1	5
241		21	9

Here we see that out of 420 moths liberated in favorable winds, 153, or a little over 36 per cent, returned, in contrast to less than 9 per cent of those in unfavorable winds. However,

we must be cautions about accepting these figures on their face value, because, we must admit, this latter per cent is made up largely by those which returned after a few hours from the dooryard.

When we consider the per cent of returns in relation to the distance traveled, these figures throw little light on the subject. Of course it is to be expected that the number of returns would decrease as the distance increases; these figures give only a poor indication of this, because of the complication of other factors.

Since I do not wish again to beg the question, I shall leave to the reader the problem of explaining the results of the series of experiments conducted on June 15, when there was no wind that I could feel, hear or detect. In this group of tests, 84 moths were liberated north, east and south of the house, of which 7 (8 per cent) returned; of 59 liberated west of the house, 21 (36 per cent) returned. Those on the west, moreover, were handicapped by an additional half-mile distance. There was obviously a marked difference in favor of the west on this occasion.

The ability, or rather the inclination, of the males that had already mated, was tested to see if they would again respond to the attraction of their mates. They appeared fully as eager and successful as the young moths. Of 56 liberated for this special purpose, 26 (46 per cent) returned. This is fully as good a showing as we could expect from any group.

There are some indications in the data that those moths which have made one or more previous flights to the roof stand slightly better chances of making another trip, or of making it in less time, than the inexperienced fliers. From the table it will be seen that of the 683 males liberated, 581 were taken out for the first time, and 102 had made one or two previous flights. Of the former, 176, or 30 per cent, returned, while of the 102 experienced fliers, 38, or 37 per cent, came back. However, here again, we must be cautious in the interpretation of these totals, because a closer examination of the data reveals that the greater number of experienced fliers chanced to be liberated in favorable winds; this advantageous factor might easily account for the slight difference in their favor in these totals. Some of the individual experiments gave stronger evidence for the superior

ability of the moths on their second or third flights, but well balanced tests with large numbers will have to be made before we can safely arrive at conclusions. And even if we find that the moths liberated for the second or third time are more successful or prompt in returning, the discovery only brings us face to face with a more profound problem, viz., are they more successful because they actually profit by their experience, or because of a finer sensitiveness and superior ability? In other words, is their superior ability inherent or acquired?

The hour of arrival of each of these 214 cynthias was recorded. It seems that each of the four species of Saturniids observed has a period of flight each night which is constant for that species.

A summary of the cynthia records reveals that for this species there are two periods of activity, a primary period from 9 p. m. until slightly after midnight, and a secondary one which runs from about 3 a. m. until a little after dawn. The peak of their activity (see Table 4) is from 10:30 to 11. Of course it is true that, early in the term of experimentation, when we had not yet fully discovered these habits of flight, we probably interfered with the natural program of these moths by liberating them too late in the evening for them to make their flight naturally that night. In a similar event, the cecropias merely waited until their regular period the next night, but the cynthias were very likely to respond to the call at their second period, about dawn. The first is probably their normal period of activity, but I am strongly inclined to think that the second is in some way influenced by meteorological or dawn conditions. A fuller discussion of this complication of primary and secondary stimuli will be taken up in the later pages on periodic activity.

It is interesting to compare the various amounts of time consumed by the different moths in making the returns from various distances. The records show the exact time for each one of the 214 males which returned, and the distance traveled. In considering the data we must not overlook the fact that where the moths did not return before dawn of the same night, since they are not active during the day, they had to wait for the darkness of the second night; so when the records show that a moth was out for 28 hours, it does not mean that this length of time was

TABLE No. 4

HOURS OF FLIGHT, CYNTHIA MOTHS

Liberated June	Experiment	P. M.								A. M.										
		8:00 to 8:30	8:30 to 9:00	9:00 to 9:30	9:30 to 10:00	10:00 to 10:30	10:30 to 11:00	11:00 to 11:30	11:30 to 12:00	12:00 to 12:30	12:30 to 1:00	1:00 to 1:30	1:30 to 2:00	2:00 to 2:30	2:30 to 3:00	3:00 to 3:30	3:30 to 4:00	4:00 to 4:30	4:30 to 5:00	Total
10	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	3	1	4
10	2	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	1	....	....	2
10	3	....	....	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....	....	1
12	4	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	1
12	5	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	1
14	6	....	....	....	....	....	....	....	....	2	....	....	....	....	....	....	....	....	....	2
15	7	....	....	....	....	....	....	2	1	....	2	3	1	....	....	....	....	1	....	10
15	8	....	....	....	....	....	....	....	1	....	....	1	1	....	....	....	1	....	....	4
15	9	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	....	....	1
15	10	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	1
Returns 2nd Night		....	....	....	....	....	....	....	....	2	....	....	....	....	....	....	....	....	....	2
15	11	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	1
Returns 2nd Night		....	....	....	....	....	....	2	....	....	....	....	....	....	....	....	....	....	....	2
3rd Night		....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	1
15	12	....	....	....	....	....	....	....	....	1	....	1	1	....	....	....	1	....	....	4
16	13	....	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	1
2nd Night		....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....	1
16	14	....	....	....	....	....	....	....	....	....	....	....	....	2	....	....	4	....	....	6
2nd Night		....	....	....	....	....	3	....	1	....	....	....	....	....	....	....	....	....	....	4
17	15	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	....	1
17	17	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	1	....	....	2
17	18	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	1
2nd Night		....	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	1
17	19	....	....	....	....	....	....	....	1	2	4	....	1	....	....	....	....	....	....	8
20	21	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	....	1
2nd Night		....	....	....	....	....	....	4	4	....	1	....	....	....	....	....	....	....	....	9
3rd Night		....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....	1
5th Night		....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	1
20	22	....	....	....	....	11	4	2	1	4	....	....	....	....	....	....	....	....	....	22
20	23	....	....	....	....	4	3	3	6	1	1	....	1	....	....	....	....	....	....	19
2nd Night		....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	....	1
20	24	....	....	....	....	....	....	....	1	4	4	....	1	1	....	....	....	....	....	11
22	25	....	....	....	....	....	....	....	....	1	....	1	....	....	....	....	....	....	....	2
3rd Night		....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	....	1
22	26	....	....	....	....	....	1	1	....	....	....	....	....	....	....	....	....	....	....	2
22	27	....	....	....	....	....	12	4	3	....	2	....	....	....	....	....	....	....	....	21
22	28	....	....	....	....	....	....	1	....	1	1	1	....	....	....	....	....	....	....	4
3rd Night		....	....	....	....	....	....	1	....	1	....	....	....	....	....	....	....	....	....	2
24	30	....	....	5	3	3	6	3	1	2	....	....	....	....	....	....	....	....	....	23
25	31	....	....	....	....	....	....	....	....	....	....	....	....	....	....	3	....	....	....	3
25	31½	....	....	....	....	....	....	....	....	....	....	....	....	....	....	4	6	1	....	11
27	32	....	....	....	....	....	10	7	....	....	....	....	....	....	....	....	....	....	....	17
Total		....	....	5	3	19	41	30	24	25	16	7	10	5	....	8	15	5	1	214

spent in search of the mate, but it does show that after an interval of perhaps 21 hours for sleep, the moth was still responsive enough to the lure to rise up and finish the quest.

The period of absence of the entire 214 moths was tabulated, to facilitate comparison of the groups which traveled different distances. The period of absence was marked off into hours for the first night; beyond that time the action of the moths was so complicated with unknown factors as to defy analysis.

Time	50 feet	⅛ mile	½ mile	¾ mile	1 mile	2¼ miles
0-1 hr.	35	14	34	0	1	0
1-2 hr.	21	13	19	1	1	0
2-3 hr.	14	4	6	0	2	1
3-4 hr.	1	0	0	0	1	0
4-5 hr.	0	0	1	0	2	1
5-6 hr.	0	2	0	0	0	0
6-7 hr.	0	1	0	0	0	0
7-8 hr.	0	4	0	0	0	1
2 night	6	1	12	9	0	2
3 night	0	0	2	1	0	0
6 night	0	0	0	1	0	0
	77	39	74	12	7	5

Experiments on *Telea polyphemus*

On May 7, I had on hand four polyphemus males, from ½ to 4 days old, but no females had yet emerged. The cecropia females were on the roof, however, and the wind was blowing through their cages toward the east. At 6:30 p. m. these four males were liberated in the park 225 yards east, to see if they would respond to a sister species. None of them came to the windows. The same test was repeated on May 20, with two young male polyphemus. These were taken ½ mile east when there was no wind stirring; they too were lost. These two preliminary tests can hardly be classified with the experiments on polyphemus, since they were only to ascertain if this species is attracted by the females of a related species. These individuals showed no evidence of such a response.

Exp. 1. May 21. Wind, northwest; station, ½ mile south. By this time I had two female polyphemus on the roof. At 7:30 I liberated 7 males, from 1 to 3 days old. Two days later at 11 p. m. one moth, the youngest one, came in.

Exp. 2. May 22. The first native polyphemus male appeared at the cages on the roof at dawn.

Exp. 3. May 22. Wind, northwest; station, 2 miles southwest. Seven males, aged from 1 to 2½ days, were liberated two miles distant. None returned in this favorable wind.

Exp. 4. May 23. With 3 females on the roof, 3 native

males arrived during the night, at 11:10, 11:35 and 12:08 respectively. These arrivals seem to be correlated with the appearance of the moon, and the details are discussed elsewhere.

Exp. 5. May 26. Wind, east, station, 1 mile west. With half a dozen female polyphemus in cages at the window, I liberated 10 males (6 aged one day, 2 aged two days, 1 aged 3 days and 1 aged 11 days) one mile west of the house. The wind was blowing from the house toward the males. Four of the 10 returned, one after 2½ hours and 3 the next night, after an absence of 24, 25 and 28 hours. On this moonlit night their actual time of arrival was 11:38 p. m., 1:10, 1:50 and 4:10 a. m.. During the period of dawn two native males also flew in.

Exp. 6. May 27. Wind, east; station, 1¾ miles west. Five native males which had come to the roof were liberated at 10:50 p. m. One came in at the following dawn.

Exp. 7. May 27. Wind, east; station, ½ mile east. Three males, all one day old, were liberated in the park, in a most unfavorable position in regard to the wind. To our surprise, after an hour and forty minutes, one returned. Another was picked up by a schoolgirl next morning, two blocks south of the point of liberation.

Exp. 8. May 27. Wind, east; station , 1½ miles east. Two native males, one old and one young, which had recently come in, were set free at 11:10 p. m. One of these wandered in three nights later, during the dawn hour.

Exp. 9. May 28. Wind, southeast; station, 3 miles northwest. When the cecropias were taken out for their long distance test, 19 polyphemus were also liberated. Four were bred moths 1½ days old, and 15 were captive wild males. Not one of these 19 ever returned. Of course the cecropias did scarcely better; only one came back, and that tardily.

Exp. 10. May 29. The night was clear, with the wind blowing from the east; at 9:00, the moon arose and remained bright. At 11:20 three native polyphemus flew in. At midnight the moon became hazy, and soon dark. Three more came in with the cecropias at dawn. This again shows that their flight is not confined to one brief period of the night, as the cecropias, but these flew for a short period before midnight and again during the dawn hour. Whether these periods are deter-

mined by rhythmic activity or by light stimuli (moonlight and dawn) cannot yet be determined.

Exp. 11. May 30. Wind, east; station, ⅓ mile east. Three native males which had come in at dawn were liberated at 9 p. m. in this unfavorable wind; none returned.

Exp. 12. May 30. The moon shone all night, and the wild moths came in at the following hours: one each at 11:00, 11:40, 11:55, 12:01; 12:05 and 3:15. Here again their activity is centered in the two periods, the midnight and the dawn hour.

Exp. 13. June 1. One more wild male came in at dawn with the cecropias.

Exp. 14. June 1. The moon that night was half obscured in a haze. One native polyphemus came in at 11:45, and 8 more during the dawn hour. This, added to the evidence of previous nights, certainly indicates two periods of activity in the night, the same as the sister species. The wind was blowing from the south, and all these moths came in from the north.

Exp. 15. June 6. During the dawn, one native wild polyphemus flew to the roof. There were 6 cages of female cecropias there, but no polyphemus; the only females of their own species in our possession at the time were on a table inside the laboratory. The arriving male spent no time on the roof, but flew in at the open window and went directly to the cage of females of his own species on the table.

Exp. 16. June 10. One native polyphemus came in at dawn.

Exp. 17. June 15. Wind, imperceptible; station, ½ mile north. The 8 bred males used in this test were 4, 2, 1 and ½ days old. They were liberated at 10:58 p. m. Only one of these returned; it was 2 days old and came in with the cecropias the following dawn.

Exp. 18. June 18. Despite the fact that the female polyphemus had been displayed constantly, since June 10 no native males had come in until this morning when at 2:20 one came and alighted on the cage. There were cages of female cynthias all about, but this male made no mistake in his selection. This is probably the end of the polyphemus season.

Summary.

Polyphemus males did not show any reaction to the many cecropia and cynthia females on the roof. No males, either native or bred, ever came to the roof excepting when females of their own species were present. During the period of experimentation, May 21 to June 18, 31 native males came in and went directly to the cages of their own species only.

Tabulation of all the data* reveals that out of the 64 marked males that were liberated at various points, only 9 returned to the roof; 7 of these were inexperienced and 2 had had previous trips. On a percentage basis, we find that 10 per cent of those taken out for the first time and 8 per cent of those that had had previous experience, returned. These figures are too small to be significant, excepting that they indicate faintly that experience is of no advantage. Of the 9 that did return, 4 came in during the first night, 3 the second night and 2 the third night.

In the small number tested for long distance flights, even in a wind which seemed favorable to them, none returned from a distance of 3 miles, or even 2 miles, but some did come back from ½, 1, 1½, and 1¾ mile points. The above evidence gives one an idea of what one may expect when more extensive work is done. It must be borne in mind that polyphemus are native to this region, and undoubtedly many of our marked bred males flew to native females. Throughout the season the native polyphemus males did not come to the roof in such abundance as did the cecropias. We do not know whether this is because these moths do not occur in such large numbers as the sister species, or whether they are not responsive to the third-floor condition, which is probably above the normal level of their flight.

The time consumed in making the trip to the roof from distances varying from ½ to ¾ miles varied from 1⅔ to 40 hours.

The normal time of flight of the cecropias was found to be (with a few exceptions under certain conditions) the hour of dawn; for cynthias, a period in the middle of the night and again at dawn. This species also has two distinct periods of activity, the hour before midnight and the hour of dawn. The hour of arrival of the 39 males, both native and bred, which flew to the roof, was as follows:

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*See Table 5.

TABLE No. 5
POLYPHEMUS

Date	Experiment No.	Time of Liberation, P. M.	Wind From	Wind Favorable	Distance in Miles	Direction from Home	Number Liberated	Number Out for First Time	Number That Had Previous Flights	Age, Days	Returned				Number Returned First Flight	Number Experienced Flighters Returned	Native Poly. that Came In
											First Night	Second Night	Third Night	Total			
May 21	1	7:30	N. E.	Partly Favorable	½	S.	7	7	....	3—1 Day 1—2 Day 3—3 Day	....	.....	1	1	1	.....	.....
May 22	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1
May 22	3	.....	N. E.	Yes	2	S. W.	7	7	....	1 to 2½	.....	.....	.....	0	.....	.....	.....
May 23	4	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	3
May 26	5	11:45	E.	Yes	1	W.	10	10	....	6—1 Day 2—2 Day 1—3 Day 1—11 Day	1	3	....	4	4	.....	2
May 27	6	10:50	E.	Yes	1¾	W.	5	.....	5	.....	1	.....	.....	1	.....	1	.....
May 27	7	11:00	E.	No	½	E.	3	3	....	1	1	.....	.....	1	1	.....	.....
May 27	8	11:10	E.	No	1½	E.	2	.....	2	.....	.....	.....	1	1	.....	1	.....
May 28	9	9:45	S. E.	Yes	3	N. W.	19	4	15	.....	.....	.....	.....	0	.....	.....	6
May 29	10	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0	.....	.....	.....
May 30	11	9:00	E.	No	⅓	E.	3	.....	3	.....	.....	.....	.....	.....	.....	.....	6
May 30	12	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0	.....	.....	.....
June 1	13	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	6
June 2	14	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1
June 6	15	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	9
June 10	16	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1
June 15	17	10:58	No Wind	.....	½	N.	8	8	....	½ to 4	1	.....	.....	1	1	.....	1
June 18	18	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Totals	.....	.....	.....	.....	.....	.....	.....	64	39	25	.....	4	3	2	9	7	2	31

11:00 to 12:00	11
12:00 to 1:00	4
1:00 to 2:00	2
2:00 to 3:00	1
Dawn, 3:20 to 4.30	21
Total	39

Thus the two periods of activity are apparent at a glance at the figures. In certain experiments there was evidence that the activity of these moths was correlated also with the moonlight, and that perhaps these moths are more susceptible to the moonbeams than are their sister species. Further tests and reactions in this line will be discussed in later pages.

Experiments on *Callosamia promethea.*

Because I could not always be on the roof in the late afternoons to study the flight of promethea, my notes are fragmentary, but are sufficient to get the time of flight and to show the trend of activities in these moths. The cages containing the females were placed both on the roof and down in the back yard.

Exp. 1. June 1. Wind, southwest; station, 1 mile northwest. The 9 male prometheas (4 bred and 5 native) were liberated in Forest Park at 5:05 p. m., in or near the path of the wind from the house. Four of the 9 returned promptly, making the distance in 10, 11 and 12 minutes and 1½ hours. The first 3 were native ones which had voluntarily flown to the roof before, and the last had emerged in the laboratory.

Exp. 2. June 10. The day was rainy and without wind. At 9 o'clock a fog formed, which was very dense by 11:30 p. m. Occasionally there was a trace of breeze from the east or northeast. At 9:14 3 marked males one day old were liberated ⅛ mile southwest of the house. None returned.

Exp. 3. June 10. Wind conditions same as in Exp. 1. Seven males were liberated in the park 225 yards east of the house. Five of these were aged 1 day, one 4 days and one 5 days. One, aged one day, came in with the cecropias at dawn. Let me state here, before the reader formulates fascinating theories about the moth that came in at dawn, instead of its usual time

before dusk, that this was the only one in any of the experiments to come in at dawn. It is easy to speculate that, since one promethea came in at the dawn period when cecropias usually fly, that phylogenetically the prometheas once had the same habit as cecropias and now occasionally revert to it.

Exp. 4. June 15. At 11:30 p. m., I liberated 26 male prometheas 100 feet west of the house, to see if they would break their set habit of flying before sunset and come back to the cages of the females during the night. Eighteen of these were ½ day old and 8 were 2 days. None came back during the night or the period of dawn, but, true to their colors, 12 came back at the appointed hour, between 4 and 5 p. m. Of those which were ½ day old when liberated 50 per cent (9) came in, and of those 2 days of age, 27 per cent (3) returned. The strongest point here is that, while they were only 100 feet away, they did not bestir themselves to come until their accustomed time, seventeen hours later.

The foregoing work on the prometheas does little more than to show that their time of flight is shortly before the close of day. Records of the bred and native males showed their period of flight to be as follows:

3:40 to 4:00	3
4:00 to 4:20	8
4:20 to 4:40	6
4:40 to 5:00	5
5:00 to 5:20	5
5:20 to 5:40	2
5:40 to 6:00	0
6:00 to 6:20	3
6:20 to 6:40	1
Total	33

It is at once apparent that of these 33 males which came in before sunset (we have socially ostracised the one who so far ignored conventionalities as to come in at dawn!) the majority centered their activity about 4:20. It is exceedingly strange that promethea should fly by daylight; at present I know of no

other Saturniid species that does so.* Here then is excellent material for experimental studies in rhythmic periodicity.

The tests have proven that it is possible for the bred as well as the wild prometheas to fly to their mates from a distance of one mile, and in surprisingly short time too—ten to twelve minutes. When part of the cages were placed on the ground, they came to those on the roof just as readily as they did to those on the ground. I have never seen these moths come in during the rain, but I have seen them come in between showers.

*Fabre gives a few instances.

PART II.

EXPERIMENTAL STUDIES ON ODOR, WIND AND LIGHT IN RELATION TO RHYTHMIC PERIODICITY IN SATURNIID MOTHS.

INTRODUCTION.

In part I of this paper, we have already seen how a tiny mass of flesh and blood called a Saturniid male braves the elements and overcomes nature's obstacles for a distance up to three miles to reach another mite of flesh and blood, the female Saturniid. In the coming together of these two masses, space is annihilated, and we seem to get a combination which is rivaled only in the chemistry laboratory. I say "seem to get" advisedly, because these moths possess sense organs which surely must function in a way that is not analogous to anything in the chemistry laboratory.

While to most organisms we accede five senses, in the case of the adult Saturniid moths we must eliminate the sense of taste. So here this organism traveling so actively toward its goal can be credited with possessing the olfactory, auditory, tactile and optical senses. Some or all of these four senses function, either in distant or proximate orientation.

What is the vehicle of the stimulus? What do these four sense organs brush up against as this tiny organic mass shortens the space between itself and the object of its flight? The atmosphere, and the vibrations which transmit light, sound and possibly other sensations of which we are not aware, since we have no organs to receive them. The atmospheric currents and gases, oxygen, nitrogen,* etc., are capable of bearing odors which can be received by the olfactory organs. Vibrations transmit the light of the moon and stars, light of various degrees of intensity from the sun, and in the city where the experiments were conducted, light from street lamps, houses and automobiles. These, presumably, can be perceived by the optic organs. Sound vibrations as a means of communication are

*In the heart of a city, many other gases and impurities.

similarly transmitted. We know from the experiments of Turner that Saturniids posses auditory powers, but we have no reason to suspect that they would function from great distances, although they might be of service in locating the female at close range. Other vibrations, akin to radio or wireless or in fact akin to the vibrations upon which our known senses function, are also carried on the atmosphere or ether. That such vibrations, as yet unknown to us, should function in bringing together the sexes, we neither affirm nor deny, but until experimental proof is offered, we place the burden of proof upon anyone who wishes to argue in their favor. So of the four familiar senses, there are two, olfactory and optical, that seem to function for distant orientation, and possibly two, tactile and auditory, for proximate orientation, the latter, of course, in addition to the olfactory and optical senses.

Now when you have at one end of the line a mass of matter which shows an affinity for another mass at the other end, and this affinity is made manifest through the functioning of certain sense organs, the masses cease to be so much inert or nonconscious matter, but become at once living, psychically endowed animals. Since this organism does respond to lights, odors, winds, etc., to the fullest extent of its being, it would be well to see experimentally if it is only a tiny mechanism that blindly reacts to environmental conditions, or if in a large number of them under observation, some individuals might display something akin to selection or emotions.

The experiments recorded in Part II were performed for the purpose of trying to discover by what means the males do find the females from a great distance, as the preceding pages have revealed they really do, and also to discover if the females are anything more than mere bodies of odoriferous substance which passively wait the coming of the males. In Part I, I have discovered to my own satisfaction that wind, odor and certain conditions of light are the environmental requisites for their coming together; in Part II, I shall try to show experimentally that they have the ability to perceive odors borne on the wings of the wind, and that they perceive light vibrations, and react to them in various ways, according to the make-up of the individuals. This combination of perception and reaction to stimuli, in con-

nection with the rhythmic periodicity of each species, leads one into entanglements which are not easily solved.

It would be best, therefore, before giving details of the experiments, to give a brief resume of the work that has been done on the rhythmic periodicity of organisms.

"Living matter is rhythmic; it is always doing something at intervals; these intervals often seem to have no relation to outside influences, like breathing or the recurrent beats of the heart, but in many cases the intervals of the acts correspond with the cosmic changes. Night and day control sleep; the tides have a marked influence on the habits of many of the shore living invertebrates, and so ingrained are these periodic habits that they are retained even when the animal showing them is removed inland and kept in a perfectly still aquarium. Summer and winter, seed time and harvest play perhaps the greatest role in this rhythm. One has only to think of the breeding habits of most animals, and the annual appearance and disappearance of the foliage of deciduous trees to recognize this." So says Arthur E. Shipley, in his introductory chapter of "Life." In a later chapter on Rhythm he interestingly touches upon various kinds and types of rhythms in both the animal and the plant world. He writes on the rhythm of cells, rhythm of parts of cells, rhythm in tissues, rhythm in organs, rhythm in organisms, and rhythm in communities.

Our general interest in the present work is rhythm in insects, and especially in moths. In Shipley's work there is no mention of this for moths. Bouvier has a chapter in his "Psychic Life of Insects," entitled "Vital Rhythms and Organic Memory," and while there is little mention of night and day activities of moths, he does discuss the work that has been done on rhythms of insects and other invertebrates from the time of Reaumur to the present day workers.

Charles Elton, in his Animal Ecology, tells us that many animals in a community never meet, because of the fact that they become active at different times. This is because the environment is subjected to a number of rhythmical changes which result in corresponding variations in the nature of the animal communities at different times. There is a day and night rhythm which affects both free living animals and some parasites. This rhythm may be of practical importance, and is

most strongly marked in the deserts. There is not always a sharp limit between day and night communities; in polar regions there is no night fauna, and in the tropics the latter is very rich.

Such night and day changes are found not only in free living animals, but also exist among parasites of mammals and birds. Owing to the fact that most mammals sleep regularly either by day or by night, there exist corresponding rhythmical changes inside their bodies, especially in temperature. In both birds and mammals, the body is slightly colder during sleep. This rhythm depends entirely upon the activity of the animal, since nocturnal birds like owls have the normal rhythm reversed (i. e., they are warmer at night), and this in turn can be reversed by changing the conditions under which they live so as to cause the birds to come out by day and sleep by night. There are certain nematodes parasitic in man which show the effects of sleep rhythm in a very remarkable way. The first species (*Filaria bancrofti*) lives as an adult in the lymphatic glands of man in tropical countries, but its larvae live in the blood. In the daytime these larvae retire to the inner parts of the body, mostly to the lungs, but at night they issue forth into the peripheral circulation, appearing first about 5 to 7 in the evening, reaching a maximum about midnight and disappearing again at about 7 or 8 o'clock in the morning. This reaction can be reversed if a person stays up all night and sleeps in the day, which shows that the round worms' activity is affected by the rhythmical changes in the conditions of the body like those described above. Another species of *Filaria* (loaloa) has larvae which live in the blood of man, but unlike the other species, these larvae come out only in the day, disappearing at night. It is stated that this periodicity is not affected by reversal of sleep, but presumably it must originally have been caused by some rhythm in bodily environment. Manson-Bahrn* mentions a third species which has larvae in the blood, which occur in the peripheral circulation equally by day or by night.

The habits of these worms have a very important bearing upon the means of transmission from one man to another; *F. bancrofti* is transmitted by blood-sucking mosquitoes which

*Manson's Tropical Diseases.

fly at night, while *loaloa* is transmitted by Tabanid flies which bite by day.

Most animals have more or less definite migratory movements during the twenty-four hours of the night and day, and in some cases these are regularly rhythmical but not necessarily correlated exactly with light and darkness. The result of these movements is to alter the composition of animal communities in any one place. Sanders and Shelford* found that among animals of a pine woods there was a certain amount of diurnal migration in a vertical direction. For instance, one species of spider was to be found among low herbs at 4:30 a. m. and among shrubs at 8:30 a. m., while another species occurred in trees at 4:30 p. m. and in herbs at 8:30 p. m.

The distinction between day and night communities is not necessarily a sharp one. The length of dusk varies throughout the year; in England it is longest in midsummer and midwinter, and shortest in spring and autumn. Again the amount of light at night varies regularly with the moon and intermittently with cloudy weather. In fact, the distinction between day and night communities may turn out to be less marked than we might at first suppose.

In polar regions there is no such alternation of day and night except during spring and autumn; and since during these times the temperature is too low or the ground too snowy to support animal life, the species living there are nearly all typical daylight ones. Conversely, below a certain depth in the sea, or in large lakes and in subterranean waters, and inside the bodies of animals, there is continual darkness, so the animals living there also form homogeneous and permanent communities. Sometimes, however, the bodies of animals reflect the rhythm of their outer environment, and cause corresponding differences in their parasitic fauna. Probably the most conservative, smooth working and perfectly adjusted communities are those living at a depth of several miles in the sea, for there can be no rhythms in the environment such as there are on land.

As we pass from poles to equator, the night fauna begins to appear and becomes gradually more elaborate and important, until in such surroundings as are found in a tropical forest it

*Ecology 3:306.

may be more rich and exciting and noisy than the daylight fauna. Tropical day and night are always twelve hours long throughout the year, while the night in southern England or northern United States is only eight hours long in midsummer.

Very little is known on the day and night rhythms of moths and butterflies. With Lepidoptera collectors almost outnumbering the Lepidoptera, it does seem strange that all we know about these activities is that moths fly at night and butterflies in the daytime. But this information is not sufficient. A day-flying moth is not in flight during all of the daylight hours, and neither is a nocturnal moth thus active throughout the night; each creature has its hours of activity; what are these hours for each species, and why are these certain hours chosen above all others? In behavior work this is an important point. For instance, Turner's careful work on behavior in the hearing of Saturniid moths with its excellent conclusions probably would have given him even better results if he had considered for each species its natural period of activity. It is logical to expect that the reactions of the moths would have been different during their hours of intense alertness and activity than during their period for slumber.

Regarding the material now in hand, we have stated in the previous pages that the cecropias become active during the hour of 3:30 and 4:30 a. m. The polyphemus are abroad from 3:20 to 4:30 a. m. and from 11 p. m. until midnight. The prometheas, for no reason which we have yet fathomed, choose to fare forth at 3:40 to 6:40 in the bright daylight, while the cynthias are active from 3 a. m. until dawn, and from 9 p. m. until midnight. Other observers have found the period of activity for allied moths to be as follows: Mayer, too, finds the prometheas active between 2 p. m. and sunset. According to Fabre, the great peacock moth requires the dusk of the early part of the night, 9 to 10:30 p. m., while the lesser peacock requires the brilliant light of the middle of the day. The banded monk or oak-egger flies between 3 and 6 in the afternoon. C. M. Weed says that cynthia moths occasionally fly on cloudy days.

Before we can determine that rhythmic periodicity *per se* is a controlling factor in these moths, we must first eliminate the reactions that are purely sensory. There is nothing we can call

purely rhythmic if the response can be attributed to sensory reaction. The following experiments will help clear up this point.

Experiments to Test Perception of Odor. (*Cecropia*).

The results of the long-distance experiments justified the assumption that the odor of the females is carried by the wind and is perceived by the male some distance away. The following close-up experiments were made to test this theory.

Exp. 1. May 18. At dawn many male cecropias came to the roof. Thirty-nine of these were placed in the glass box.* The temperature was 68° F. In an hour they were all quietly settled; then I gently placed two females (each in a small wire cage), aged 4 and 8 days, in the box. This change elicited absolutely no movement on the part of any of the individuals of either sex; all rested so quietly that they appeared in profound sleep. The females were not expected to be aggressive, and the males may have been fatigued after their long morning flight over the roof-tops to reach the cages. At 7:17, after a lapse of 17 minutes, the young female began slowly to move about, then suddenly vibrated her wings in a very excited manner. Within a very few minutes, two males nearest her cage too became thoroughly excited. As she continued rhythmically vibrating her wings, another small group in the opposite dark corner began to show activity. (The glass box was at this time covered with a heavy blanket, which was lifted from one end, thus admitting the dim light of a cloudy day. The males were all near the dark end of the box, and the females in the center.) As the fluttering of the few males at the dark end continued, I thought they would settle on the cages of the females in the center of the box, but therein I was mistaken; all those which were aroused to activity fluttered past the females and on into the light portion of the box, and there fluttered violently up and down, bumping their heads against the glass. When the females rested a few minutes later, I counted eleven males struggling against the glass at the light. The males, aroused from quiescence at the dark end of the box by the agitation of

*This glass box used throughout these experiments was a thirty-two-gallon aquarium with glass sides and iron bottom; either a glass or an opaque cover could be improvised as desired.

the females, all flew past the females, ignoring them en route, and crowded to the light. Not all the moths behaved alike; only 11 out of the 39 responded thus. This may be explained by the fact that this was an off hour for their activity, or by the hypothesis that physiologically and psychologically, the moths show individual differences. This demonstration shows beautifully that it was not the females *per se* that aroused the males, but the odor that emanated from their bodies after they had begun to vibrate their wings, and the reaction of the males, after having been aroused by the circulating odor, was to fly to the light. There were still 28 males that remained unaffected at the dark end, the same area from which the 11 active ones had come. Why did they not respond? I placed the two females in their individual wire cages in the midst of this group, but they failed to stir. I prodded the young female with a pencil and soon she became intensely active again, vibrating the wings rapidly. This aroused to activity some of the 28 males near her, and almost simultaneously the eleven at the lighted end, which had been quiet for a time, renewed their agitation, rapidly vibrating the wings as they moved up and down the glass and beat their heads against the barrier.

Before this one young female had vibrated for one minute, three of the 28 males left the crowd and joined the eleven at the light end of the box. These were quickly followed by other males, and when she quieted down after two and one-half minutes of vibration, there were only 14 left at the dark end of the box. Even during the ten minutes following, 6 more males responded to the disturbance and flew to the light side, leaving only 8 unaffected by her influence. I tried again to prod her to activity, but there was no response, perhaps due to fatigue. So here were 31 out of 39 males responding to the excitement created by this female becoming active and beating the air with her wings, while all had been stolidly indifferent so long as she had remained quiet and there had been no circulation of air in the box, although she was very near to them. The males did not all react at the same time; some responded to the stimulus promptly, and others much more slowly. This may indicate that some of them were out of the path of the circulation of the air at first, but it seems to me more likely that some males

are less sensitive, and hence harder to arouse than others. The fact that some males were aroused almost simultaneously with her first wing movements, and at the end 8 were still indifferent in the same environment suggests a wide range of individual differences in a very essential character in the life of the species.

These males were native moths which had flown into the laboratory at dawn that morning; in the next experiment we shall study a similar phenomenon with males bred from cocoons in the laboratory which have had no outside experience; hence any possibility of the interference of fatigue will be eliminated.

Exp. 2. May 29, 11 p. m. In the glass box I placed 41 male cecropias which had emerged in the room; 14 were ½ to ¾ day old, and 27 were from 1 to 1½ day old when they were placed in the box at 11 p. m. Since the males in the last experiment had shown such positive reaction to the light after having been awakened by sex excitement, it was decided to test these for their reactions to the light alone before introducing the females into the game, to see if after spending a period in absolute darkness they would react to light rays when no female odor was present. The whole box was darkened by covering with several layers of blankets and roping these about the table legs so not even a pencil ray of light could penetrate from below. At 10:10 the next morning, I found 32 males precisely where I had left them, and 9 had wandered about a bit. This little incident shows of course that if they become active each night at stated hours because they are instinctively attuned to do so (rhythmic periodicity), then all or the majority of them would have changed their positions, especially since during this period of confinement in the box (from 11 p. m. to 10:10 a. m.) they passed through this time when they are usually active. Hence in the absence of light or sex stimulus, their rhythmic periodicity failed in this case.

When the blankets were folded back from one end of the box, at 10:10 a. m., one male immediately became active, and after ten minutes two more were wildly fluttering the wings; these three moved to the light end, while two more at the rear (dark) end slowly moved their wings up and down. This is the sum total of the activity of 41 males for a period of 30 minutes after

the mild light of the room was admitted at one end of the box. I then created another period of darkness by covering them securely for 35 minutes. The cover was lifted again, and during a period of 30 minutes not one of the 41 males had moved an iota. All of the males were then shifted, as gently as possible, to the rear end of the box, and a wire cage containing five young females (aged 1½ days) was placed at the light end. One female proceeded to slowly open and close her wings, and during the following ten minutes five males flew to the light end and beat against the glass wall. Then a second female began to vibrate her wings, and in five minutes three more males came out of the dark end and joined in the excitement at the light end of the box. With the activity of the males very near to them, the excitement of the females ran high. If one suspects that cecropia females are entirely devoid of emotions and that they mate only by virtue of being passive bundles of odoriferous substance, let him watch a group of females placed as these were near a group of excited males. First one and then another would flutter or vibrate the wings with great rapidity for a few minutes; this was followed by a wave of intense excitement on the part of the males—one is tempted to call it an agony of desperation. The females in their little cage were near the light end this time, instead of in the middle as before, and the males paid more attention to them than they did in the last experiment, and many attempts at mating through the wire were made. Strange to say, the females were the more agressive in these attempts. At noon the excitement was still high, but by 12:15 all had subsided to quietude, with 12 out of the 41 at the light end of the box.

Thus these five females were able to arouse only 12 out of 41 young males in this case. This is a much smaller proportion than in the last experiment. The cause of this difference remains a question; there are several possible reasons. First, our day-time is their midnight, and we could not expect them to be active during their normal period of rest. Second, the males may have been too young to be as sensitive and responsive at this early age. Again, these had emerged in the laboratory and had never had any out-door experience with either the extremes and variations of light and darkness, or in responding to the

female emanations. This would imply that experience aids and augments instinct in this activity—a hypothesis which we mention but shall not champion at present. Lastly, the moths used in this experiment were a random sample of the population, that is, all that emerged from a certain lot of cocoons, while the males in the preceding experiment had in a way selected themselves from the whole population of wild cecropias in having found their way to the roof the first time from the wilds; in this preliminary test any of their brothers who were too weak or stupid, or did not possess the delicate sensitiveness to respond to the call of their mates were of course left behind in the woods, so those which responded so obligingly for us in the last experiment had really been selected by Nature for this very activity, and had proved their ability. This latter condition appeals to me as a more plausible explanation for the difference in the response of the two groups of males than either of the two former factors. This difference in the reaction of the two lots of material here shows clearly the danger of drawing sweeping conclusions from material of unknown history. Here two lots of material, outwardly alike, have psychological states, and possibly also physiological foundations, quite diverse.

Exp. 3. This is a continuation of Exp. 2. At 12:15 p. m. the females were removed and the box darkened with blankets in the usual way. For seven hours the cage was left so, and at 7:10 p. m. the south end was uncovered. There I saw all of the moths in a state of profound quiet, apparently asleep. The room was lighted by a 50-watt lamp hanging from the ceiling twelve feet away, and in front of the uncovered end of the box. When the curtain was lifted a few of them started to flutter about, and after ten minutes seven of them had assumed activity of some sort. In 25 minutes, this number had not increased. This surprised me, because they had now had a long period of rest, and instead of midday it was almost night, the time when one would expect them to be aroused easily, even without artificial stimulus or the presence of females.

The males, now all quiet, were placed at the dark end of the box, and at 7:50 a wire cage containing 8 healthy females was placed in the light end. The females remained quiet, almost motionless, and after three hours only 6 males had worked their

way to the light end. At 11:10 I approached cautiously and fanned a current of air over the cage of females and toward the males in the dark end of the box. Almost immediately many wings began to quiver, and in five minutes 13 more had wandered to the lighted pane. The fanning was continued only at intervals, but up to 3 o'clock no more had responded. This shows that the males may remain in the presence of female odor plus light and only 6 out of 41 stir in three hours, whereas in female odor plus light plus breeze, 13 more respond within five minutes. But in this test again where moths bred in the laboratory were used, more than half of the males failed to react at all. How is this to be explained? Are these laggards the stupid ones which Nature would eliminate in the wilds?

Exp. 4. June 3, 2:30 p. m. Thirteen young males were gently placed in the box with 32 females; all were quiet at the time. Heretofore, the females when placed in the glass box had been enclosed in a wire cage, but this time they were all placed together free. For 45 minutes there was no reaction of any kind by any of the moths of either sex. Then I began to fan the group gently with a folded newspaper; after about five minutes of this a few males awakened to gentle response, and then two females; in ten minutes more, five females were participating in wild fluttering, and three of these had done just as the males in previous tests had done in fluttering to the light end of the box, and there beating their heads and wings against the glass nearest the light. Whenever their activity lessened or ceased, a little fanning would quickly arouse them to renewed activity.

This experiment shows, as did some of the previous ones, that some females do show aggressiveness, react to light vibrations, and possibly also are influenced by the emanations of the opposite sex, just as are the males.

Electric Fan Experiments.

In the foregoing experiments we have seen how, ordinarily, quiet moths are not influenced to activity by the presence of the opposite sex in close quarters until a breeze, either artifically induced or naturally created by the flapping of wings, disseminates the odor. The following supplementary experiments were made upon moths of both sexes in separate cages placed before

the steady stream of air from an electric fan. These tests give us data on: (a) the reaction of male moths when placed before an electric fan, (b) the reaction of female moths when placed before an electric fan, (c) the reaction of male moths when female odor was blown upon them, (d) the reaction of female moths when male odor was blown upon them. Since each of the experiments gives data on more than one of the above four points, it is not possible to classify the work under the above headings, but the experiments are given in the order in which they were undertaken.

Exp. 5. May 30, 12:30 p. m. A cage containing 10 male cecropias and one male polyphemus was placed in front of an electric fan, which was set to the slowest possible speed to throw a steady flow of air. All these were native males that had come in with that morning's dawn. For fifteen minutes they were subjected to the slow, steady stream of air from the fan. There was absolutely no voluntary action or reaction on the part of any one of the males during this period. The motion of the air would sometimes force a wing to one side for a moment, but there was no voluntary movement. The only reaction, if it may be so called, was that the males clung the more tenaceously with their tarsi to the meshes of the cage. The fan was turned off and they were given a rest of 15 minutes.

When the fan was turned on again, a cage of six females, from one to two days old, was placed half way between the fan and the cage of males, in such a way that the breeze would pass through it before reaching the males. After just two minutes of the rain of this tainted air on the erstwhile motionless males, 3 began vibrating the wings with intense rapidity, and in five minutes the male polyphemus was fluttering wildly about (for a cecropia female!) and another cecropia joined in the activity. During this period of ten minutes there were four other males which made, not a frantic demonstration, but a gentle movement of the wings up an down. There were only two which showed no response to this modified air, whereas a little while before none of the lot showed even a slight response to a breeze of the same intensity of pure air. When the fan was stopped, the moths soon became quiet; after a ten-minute rest the current of air was renewed, very gently; this revived their activity and within five minutes all but one male showed some reaction

to this stimulus, either by flying about, fluttering or waving the wings.

To again see if they would act in the same manner in a breeze of clear air of the same strength, I gently removed the cage of females from the path of the breeze. There was no period of rest given the males between these two trials, but when they were in their greatest activity the cage of females was gently slipped away. It was interesting indeed to see that in just three minutes, eight of them became quiet, and in two minutes more the other two subsided. And so they continued motionless, even when the breeze gently pushed a wing this way or that. After a quarter of an hour, the cage of females was again pushed between them and the fan, and within five minutes three males were in a state of excitement. The fact that the response was not so general this time may have been due to one of three things: the males may have been fatigued; they may have become accustomed to this stimulus to which they could not normally respond while imprisoned; or the wind from the fan may have had a cooling effect on the pores or organs of odor of the females and reduced their efficiency.

This experiment substantiates the results from the glass box experiments, and the theory that the males come great distances to reach the females by following the odor on the wind. This test indicates also that not all males react in the same way, but while this seems to be so, we must be cautious about saying it with too much positiveness because with our crudely improvised technique it seems quite possible that the odor-laden air was not equally distributed over the entire cage. These reactions, please remember, were not made at the hour of their natural time of activity, which is early dawn, but at high noon, which is their midnight. These males were wild native ones which had come to the females on my roof; it would be interesting to see what responses we would get from males which had emerged from their cocoons in the laboratory, in other words, a strictly random sample, unmodified by experience or selection.

Exp. 6. May 30. 6:25 p. m. This experiment was made upon 18 males which had come in at dawn of the day before. The fan was placed three feet away, and a stream of pure air was thrown upon them. After ten minutes of this treatment,

there was no movement or any other indication that they were aware of it, just as in the previous experiment.

A cage of ten females from one to two days old was gently inserted between the males and the fan; after five minutes, six males were opening and closing their wings. After a few minutes, four of these relaxed and only two remained active, one of which escaped and flew out the open door. Not content with the slowness of their response to the magnificent treat which I was offering them, I suspected that through poor technique much of the odor was missing the mark, or more likely, was being carried through the cage of the males too quickly. Therefore I built a wall of books and boxes behind and beside the cage, so this air could be retarded and would accumulate. Two minutes after this change was made, several of the moths began to vibrate their wings, and five minutes after the wall was done, five males were beating their wings in intense excitement, and all were struggling against the side of the cage facing that of the females. Of course, it appeared that they were pushing their way toward the source of their excitement, but we must consider also that the window was in that direction, so it may well be that, after having been aroused by the odor stimulus, they were struggling to go toward the light, as the moths did in similar circumstances in the glass box. After seven minutes of this arrangement, six were active; after 13 minutes, eight were excited, and since no more of the 18 showed signs of responding, the experiment was concluded. Thus retarding or piling up the tainted air caused eight to become violently active, whereas in the first part of the experiment, six (four of which soon relaxed) made only a languid response.

Exp. 7. This is really a continuation of Exp. 6, excepting that the sexes were reversed in their position before the fan. Heretofore the females had always been so placed that they received only the pure air direct from the fan, untainted by male odors. The reactions of the females, when the pure air passed through their cage, was exactly the same as it was for the males under similar conditions. Their only reaction, if it might be called such, was to cling the more tenaceously to the meshes of the cage. The wind often pushed a wing to one side, but there was no voluntary response on the part of a single female to a current of pure air.

Now the cages were shifted, so the air was blown from the males upon the females. Within a few seconds after the exchange of positions, the hitherto active males quieted down in the breeze of pure air and remained motionless; the females, now placed in the stream of air from the males' cage, just as readily showed response. Within two minutes, four of the ten, heretofore stubbornly indifferent, became violently active, and in five minutes two more gently responded. The others remained unmoved up to the conclusion of the experiment ten minutes later.

This experiment shows clearly that some of the females do respond to the odors of the males, and the proportion of these compares well with the proportion of females which responded when the air was agitated by fanning in the box experiments.

Exp. 8. June 3. The material was 12 male cecropias which had come in that morning at dawn, and 22 from the previous morning. The two cages were placed side by side, with two cages of females from one to three days old between them and the fan, as in previous eperiments. However, before the females were placed there, the stream of pure air was permitted to play upon the two cages of males for an hour. During all this time there was not a quiver of response, although at times the strong breeze deflected the wings. Almost immediately after the two cages of females were placed between the males and the fan, there was very active response among the 22 males which had come in the day before; this activity soon developed into a very excited flapping and fluttering, and was participated in by almost all of this group; this riotous excitement lasted for fifteen minutes. The 12 moths in the other cage, which had come in at dawn that morning, were strangly different; despite the fact that they shared equally the wind as it came from the cages of the females, and despite the fact that their cage touched that of their neighbors where they could undoubtedly hear, see and smell the activity, there was absolutely no reaction on the part of even one male. I am at a loss to explain this exceedingly strange behavior; if it were not for the fact that other males responded to such stimuli in experiments conducted during their first day in the laboratory, one would conclude that the fatigue of the flight that morning had made them numb to sounds, odors, etc., whereas those

which responded had had a longer period in which to rest. However, this lack of response gives us some evidence in another problem. In going over the experiments, one might expect that activity in some cases might be due to imitation, that the activity of one moth in a group influences the rest to motion, that movement to light or odor might not be due to light and odor *per se*, but merely to sharing a neighbor's excitement by imitation. Here we see 12 males remaining immovable, even in close juxtaposition to 22 very active ones. This indicates that each male asserts its prerogative of being a separate entity, physiologically and psychologically, and reacts only when he himself is ready.

Exp. 9. In this experiment, the positions of the cages were reversed and the actions of the 20 females observed. When the pure air was passing through their cages, they made absolutely no response of any sort. As soon as the cages were transposed and the air from the males came upon them, there was a startled stir; for five minutes three females quivered their wings, then there was not further action although the breeze was continued for twenty more minutes. Thinking that possibly the wild life that these males had led might have depleted their attractiveness, and not knowing how old they were, I removed these two cages of wild males and put in their place two cages containing 27 males that had emerged from their cocoons in the laboratory two days before. For forty minutes the breeze from these was blown upon the females, but not one would stir. Here too it is apparent that the response to stimuli is not extraneous, but occurs only when the individual insect is ready physiologically.

Exp. 10. This was not a set experiment, but certain accidental discoveries were made on the wind, odor and mating which should be recorded here. They seem to show that wind is necessary for proximate as well as distant orientation; in other words, even though the male is close to the female, the wind is a factor in bringing them together.

On June 3, at 6 p. m., 26 wire dish covers, each containing a male and a female from 1½ to 3 days old, were arranged on a table back in a corner of the room. I needed a number of fertile females for another experiment, and I thought, of course, I could get them in this way. Mating usually occurs in the

early hours of morning. The next morning I was surprised to find that only six pairs had mated, and four of these pairs were at the edge of the group of cages nearest the open window. On another occasion when six young males were placed with 32 healthy females in a large box with close-fitting glass lid so all circulation of air was excluded, only one pair mated. In contrast to these incidents, a cage on the roof blew over one morning, and in a very short while, before the females had had time to fly away, they had all mated with the native males which were coming in. These accidents seem to indicate that close proximity of the two sexes is not in itself sufficient to bring about the union unless a circulation of air plays upon them and assists them in locating each other.

Exp. 11. This too is only a group of observations pertinent to the subject in hand. That each of the five species of Saturniids has a specific odor no one will deny. The odor of any one species is perceptible to the human olfactory organs, but if a difference exists in the odor of the two sexes of each species, it will take a very acute sense to distinguish between them. The following notes, meager as they are, will throw some light on the subject.

On May 6, when I entered the laboratory, I immediately perceived a strong cecropia odor, although there were only fifteen moths of both sexes there, and five windows on the east and west walls were all open. This shows the heaviness of the odor and its staying qualities. From this time on it was no uncommon thing for the members of the family, when on the street in front of the house, to catch a strong whiff of cecropia odor on the breeze. Moreover, on several occasions when they were out riding, they would pass through a "streak" of cecropia odor in the atmosphere; in these cases the odor seemed actually to form a distinct, clear-cut stream through the air, like the Gulf Stream through the Atlantic. My wife sniffed the limits of one such stream and found it, according to her olfactory sense, to be about fifteen feet wide, and distinct enough that she felt sure that she could have followed it back against the breeze to its source if the traffic on Pennsylvania Avenue had not been so heavy at that point. Of course she had no way of knowing whether the moths were near or far. This characteristic form of dissemination of the odor is of im-

portance in an understanding of the quest of the male. If the odor were light and volatile, and diffused in all directions equally, like ripples on a pond, there would be little chance for the male to locate the source. The course followed by the moths in approaching the roof where the females are gives slight indication of the nature of these emanations. Sometimes the males would approach from a distance flying near to the ground and only when near to the house would they turn their course upward and over the edge of the roof; at other times they could be seen for some distance flying at the level of the second-story roof.

At one time the only females that we had out on the roof were those which had hatched from the New York cocoons, yet for several days the native Missouri males flew to them in great numbers; this would indicate at least that the odor was not noticeably different in the moths from two widely separated localities. Of course, one would only expect that geography would make no difference in the odor glands of the moths, but so many queer things happen in nature, and so many unexpected factors have come to light in the details of the present problem, that I am glad of the opportunity to know positively that Nature substantiates our expectation in this matter.

When many cages containing female cecropias were on the roof and there was more choice for the males, they spent much more time fluttering and hesitating before alighting. Early in the work when there were only three cages of females at the window, the flight of the males was very direct, but when the odors emanated from a dozen cages scattered over the roof, the males had difficulty in choosing the desirable cage. Quite often they would spend from two to five minutes fluttering about the roof, apparently in confusion. In several instances the males were seen to fly in a straight line past the roof and a few feet beyond; then, apparently discovering that they had gone too far or at least lost the trail, they turned squarely around and retraced their wingsteps to the right place.

There were on the roof at one time three cages containing polyphemus females, but not one of the cecropia males ever made the mistake of even alighting on one of these. Likewise, although polyphemus males came to the roof occasionally, they did not rest on the cages of the other species. The relationship

between cecropia and cynthia is closer, for there was an interspecific attraction and on one occasion a mating. Other investigators have found it possible to cross cynthia and cecropia and get fertile eggs.

Exp. 12. Everything so far points to the probability that the males find the females through odor perception. The problem whether certain females are more attractive than others to the males remains open. If odor is the medium of attraction, it seems to me that the degree or intensity of odor would be to a great extent regulated by the age of the female. With this in mind, the following tests were made on cecropia:

Six cages were arranged in a row (see figure 1); each contained 10 females, whose ages were as follows:

Cage 1, ½ day old.
Cage 2, 1 day old.
Cage 3, 3 days old.
Cage 4, 4 days old.
Cage 5, 5 days old.
Cage 6, 6 days old.

The cages were placed in the path of the wind, and betweeen 10 p. m. and 4:30 a. m., 26 males flew to them. They did not always remain on the cage which first attracted them, but they were counted as being attracted to the cage upon which they finally rested. The following table shows how many males were attracted to each cage:

Cage	Age	Males	Cage	Age	Males
1	½	3	4	4	6
2	1	11	5	5	4
3	3	2	6	6	0

Thus the males clearly decreed that in their estimation the females which were one day old were the most attractive, while the antiquated females were spurned entirely. In some of the earlier experiments some of the old females still attracted males, but on these occasions no younger rivals were present.

While the majority of the males flew direct to the cage from which they were recorded, several flew to various cages, testing out, as it were, the qualities of the inmates before alighting. If an adherent of the theory of chemotropism still thinks that the males are drawn to the females as iron filings are drawn to a magnet, let him weigh and consider some instances which I observed in detail.

At 10:50, male No. 18 flew to cages 5, 3, 2 respectively, and then flew away. After a few minutes he returned and fluttered again, this time stopping at cages 2, 5, 4, 2, and then a second time flew away; returning a third time he flew to cage 2 and soon settled down to remain there.

At 11:30 p. m., male No. 33 flew to the roof and fluttered for several minutes each at cages 4, 5 and 6, and then flew away; returning he examined cage 4 again and soon settled down to remain there.

At midnight cecropia No. 54 appeared and fluttered about cage 6, then 5 and flew away; for some minutes he fluttered about neighboring roofs and then came back as if following a new trail and alighted on cage 2 where he remained.

At 12:50 a. m., male No. 303 examined cages 6, 5, 4 and 3, and finally chose 4.

Between 1:00 and 1:05 three males came but flew to the brick wall, to a cranny under the third floor guttering, where they behaved as though they were looking for something, and then flew away. Closer examination revealed that the breeze blew from the cages toward the wall where the air was caught in this pocket or nook under the guttering. The males probably congregated where they found the odor, although they were deceived as to the location of the females.

At 1:20 male No. 52 fluttered about cage 5, then flew away; returning presently he went to the same cage again and alighted there.

At 3:22 a wild male fluttered for a long time about cage 2 and finally settled on cage 1; a few minutes later another similarly examined cage 1 and eventually rested permanently on cage 2.

Experiments to Test Reaction to Light.

We have seen in the previous experiments testing the perception of odor that reaction to odor stimulus occurs only when wind is present to convey it. These experiments have shown also that when moths have been aroused to activity by odor of the opposite sex, they react usually not to the individuals of the opposite sex directly, but fly to the light, even though they must pass their mates to go there.

The following experiments will show that odors are not always necessary to induce reaction to light; that under certain conditions of light the moths will react to it.

The tests were made to see to what degree the recurring rhythmic periods can be changed. In *Samia cecropia*, the period has become fixed (with certain exceptions) at the hour of dawn, or between 3:30 and 4:30 at this time of year. In so far as light conditions are concerned, this period covers all the degrees from blackest night just preceding dawn to the light of day just before sunrise. The idea in this work was to create at various hours during the twenty-four a condition of diffused light in as close imitation as possible to that which caused their reaction at dawn. For a long time preceding these imitation dawns, of course, the moths were kept in darkness, to make more realistic these make-believe dawns at various times of day.

The statement is made by Reamur** that "most of the night-flying moths which are at liberty in the country fly only at night or on the approach of night. Some, moreover, of the same class when kept enclosed in boxes or cages show the time when their inclination leads them to flight. During the day they are quiet in their prisons, passing hours, often days, without moving, in the same place. But when night had come, even before the sun is ready to set, they move their wings and are ready to fly as much as their box will permit."

Without having access to Reaumur's original publication, one does not know to what species he refers; however, my work thus far indicates that night-flying moths, at least those herein referred to, do not fly at all hours of the night, but the statement that when they are enclosed in dark boxes they "show the time when their inclination leads them to flight," and "even before the sun is ready to set they move their wings and are ready to fly" cannot be accepted without further observation. The following experiments will show whether in a really dark compartment the moths become active with the recurring period of their normal activity. They will also show if these periods of activity can be changed by artificial conditions.

During the early morning period of activity, seven male cecropias had flown into the laboratory. As very often happened when they flew in from the west, we found them at rest,

**Bouvier, Psychic Life of Insects.

not on the cages of the females, but on the windows facing the east where the first rays of light penetrated. These wild moths were placed in a wire cage, but when handled they became very active and beat their wings against the mesh so harshly that for their safety they were transferred to the big glass box. This box was darkened with several layers of blankets on three sides, top and bottom, but all of the moths continued their activity at the open end. After five minutes, I covered this end and opened the opposite end; within two minutes all seven of the males had fluttered to the newly lighted end. After three minutes, this end was darkened and the first end again uncovered; almost immediately six of the seven flew back to the light end and continued their activity. While they were still active during a period of five minutes, I suddenly threw off the cover, permitting the light (the ordinary diffused light of a room on a clear day) to freely enter the box from four sides and top. I imagine their interpretation of this sudden flood of light was that daylight had come and it was time to rest, while the previous condition, dim light from only one direction and elsewhere darkness, had seemed to them dawn, for almost immediately all of the moths quieted down and rested calmly. The actions of these cecropias under these experimental conditions look at first very much like a case of pure phototropism. This simple experiment shows that they are sensitive to differences in degree of light (differential sensitivity), but whether the creatures react to certain light waves in a fashion entirely mechanical, I think the work as a whole will disprove.

But to resume the experiment, the moths were still exposed to the full light of the room, and all were quiet. So they remained for half an hour when two of them resumed activity, fluttering toward the light, despite the fact that there had been no disturbance or change in conditions that I could perceive. Then I covered the box entirely excepting a small peep-hole through which I could see that it took these two moths just two minutes to subside into quietude under these new conditions. After another half-hour the cage was again completely uncovered, but this change called forth no response. Whether this indifference was due to their fatigue, or whether strong light was as much an inducement to sleep as profound darkness, I cannot say.

Exp. 14. The seven moths mentioned above plus three more wild ones were allowed to rest until 5:30 p. m. the next day; the box was carefully covered to exclude the light. In the late afternoon, 5:30 p. m., the daylight was supplemented by a 50-watt electric light about twelve feet from the box. After having gently placed all the moths at the dark end of the box, the curtain was lifted at the end nearest the light. In three minutes, three males had made their way to the lighted end, and after ten minutes I counted seven there. This movemnt was certainly due to the difference of light and not to the period of day, for this was not their normal time of activity and the controls in other cages did not show any activity at that hour. Of course the controls were exposed to the light of the room all day.

During the forty minutes when the moths were subjected to the light from one end of the box only these seven responded to the lure of the light, so at 6:10 the moths were all quietly placed at that end of the box and covered, and the blankets lifted at the opposite end, which was not so brightly lighted since it did not directly face the electric light. During the first ten minutes, three males fluttered to the lighted end, and after twenty-five minutes, eight were there. These did not flutter so wildly as they had done in the first part of the experiment, but one cannot expect intense activity indefinitely. But their sensitiveness to the light was unquestionably demonstrated first by their going to the lighter end of the cage, and second by crowding into the lightest corner of that end as they settled to rest. Some critics might say that a part of this activity may be attributed to imitation; that a few of the moths are supersensitive to the rays of light and become active on slight stimulation, and the others follow by imitation or simply by being disturbed. This is by no means the first experiment in which we have found that a small proportion of the moths remained persistently quiet while their brothers all about them became active; hence we have reason to believe that each individual reacts when and only when he himself is physiologically or psychologically ready.

Exp. 15. The above was of course a test of the reaction of the moths to the dim light; now we shall see if they react likewise to bright light. If the dim lights and shadows of evening

and early dawn lead the males to activity in the open, natural environment, and if the bright light of day induces them to rest or perhaps sleep, as it does the owl or bat, one would expect the same results in laboratory tests.

With this question in mind, at 7:30 p. m., a 75-watt electric lamp with a reflector behind it, was placed flush against one end of the glass box, while the moths were all at the other end. Almost immediately one moth flew into the light until it was stopped by the glass. This particular male was, it seemed, supersensitive to light, for he was without fail, the first one to react in every light experiment; he was easily to be distinguished from his companions by black pubescence on his head. After ten minutes, two more responded, somewhat languidly, and then no more came. These three were marked and replaced at the dark end with their companions. After five minutes two of these were at the light again, and after two minutes more the other marked moth joined them. In a previous experiment, eight out of ten responded to dim light; here only three out of ten responded to bright light. This shows clearly that the majority react to dim light, while only a small proportion are attuned to the high intensities. One wonders what were the eccentricities or the special endowments of the one individual with the black pubescence that enabled it or drove it always to respond first to the lure of the light, both dim and intense, while many of his brothers rested.

One might suspect that fatigue came in about the time this test with the bright light was begun, and that for this reason few responded. To test this point, I repeated the first part, after having kept the moths in the box in darknesss for an hour. I then placed the moths in the north end, and uncovered the south end of the box next to the small lamp twelve feet away. Within ten minutes, eight again out of the ten responded to the stimulus by flying to this end. Then I repeated the bright light test, placing the 75-watt lamp against the end of the box after shifting all of the moths to the other end; it took just twenty-five minutes to bring one moth to the light, and no others followed. Once more I tried the dim light. Within two minutes, two of the moths reacted, and after ten minutes six were there and the other two registered their response by flapping their

wings. By this time I was convinced that these happenings were to be accepted as action and not accident.

Of course the dim light was some distance away and the bright light flush with the side of the box. Now the questions come to mind, whether the insects were far-sighted or near-sighted, and what difference would their vision make in their reactions. Unfortunately, no experiments could be made at that time to learn their response to a bright light at a distance.

These laboratory experiments on the reactions to light bring us again to the puzzling question which probably will never be answered. In the open these males fly past street lamps, house lights and numberless automobile lights in order to reach my laboratory to meet the females there. Then when in that laboratory, they are so influenced by light rays that they leave the female nearby and passionately beat their wings on the window toward the light until they die of exhaustion.

Of course this experiment shows also the futility of trying to account for this behavior by phototropism. If the reactions were actually phototropic, then all of one lot should react, or not react, but all in the same way while under the same influence. Loeb in citing his instances for animals of various orders says they did or did not react thus and so. He does not take into account exceptions, individuals that did not go with the crowd, and we assume that none existed. But here in this work we do find exceptions, and these exceptions should not be overlooked. A chain is as strong as its weakest link, and the theory is weakened just in proportion to the number of exceptions.

Exp. 16. May 21. The purpose of this experiment was to test on a larger scale the reactions of cecropia males to light of weak as well as strong intensity. Seventy-eight males came in at dawn that day; these were all placed in the large glass box and kept tightly covered with blankets.

At 3:15 p. m., the cover was lifted at one end. The light at that time was the ordinary light of a room with two east windows. Almost immediately some of the moths began to vibrate their wings, and in five minutes about three-fourths of them registered some response. Some waved the wings, others fluttered to the light end, and many crowded and beat themselves against the glass in great commotion. The vibration of

so many wings created a loud humming noise. Many of the males kept their antennæ in excited motion much of the time, and in one case an individual crowded near to the glass and pulsated his abdomen in unison with his wings.

Seven minutes of this activity gave all the evidence that we needed, so I darkened the box again; almost immediately the hum subsided, and quiet reigned. This condition continued for thirteen minutes. Then the cover was lifted at the opposite end and the strong light, the 75-watt lamp with aluminum reflector, was placed against the outside of the glass. It was three minutes before any of the 78 moths showed signs of response, and then only two slowly vibrated their wings. After seven minutes, eight were waving the wings; three of these came to the light. After being subjected to this dazzling light for ten minutes, five were flying against the glass part of the time, and part of the time they flew back into the corners away from the light. One more male occasionally moved a wing. Thus of the 78 moths, only 6 made response to intense light, and the majority of these responses seemed half-hearted or confused, and in a few minutes, even while the light was upon them, these settled down to quietude. After a quarter of an hour it was evident that the show was all over, so the cage was again darkened. An hour later it was opened again at one end to see if a larger number would now respond to a mild light (that of an east room at 5:00 p. m.). Immediately when the curtain was lifted, three moths broke into fluttering, and in three minutes three more were beating against the glass at the light end. After the cover had been up ten minutes, twenty moths were doing various antics, as before. It was growing darker in the room now, and rather than turn on the electric light (since this was to be an experiment with subdued natural light), I admitted more light to the box by lifting the curtain on one side in addition to the one end that was already exposed. In five minutes more than half of the inmates of the cage had joined in the excitement, but after eighteen minutes many of those which were first active began to slow down and a few became quiet. Here again we find much greater response to diffused light of low intensity than to intense light. To the moths, doubtless the opposite extremes in the intensity of light mean correspondingly opposite behavior; brilliant sunlight or its counterpart is

correlated with sleep or rest, while dim light suggests to them activity and mating.

In other cages nearby while this work was in progress were moths of both sexes bred from cocoons in the laboratory, and other native males that had been attracted by our females, but none of these showed any signs of activity at this time of day. They were exposed all the time to the normal changes of night and day, and their program was not disrupted by artificial imitations of darkness, daylight and dawn. Hence it appears that the activity of these creatures is regulated by the changing intensities of light and not, as has been thought by many investigators, by the clock. Of course it was not the normal time for activity of those in the glass box, any more than it was for the others in the room, but they were easily fooled into activity by fake dawns, at any time of day we wished to stage them, so long as we did not work them to the point of fatigue. The fact that their periods of rhythmic response is altered by light conditions shows that this habit is not so deeply ingrained in their psychology (or is it their physiology, or is it both?), else it could not be so readily changed. The fact that cynthia does not so readily change its periods under similar conditions makes one suspect that cynthia is phylogenetically older, since her habits are more deeply ingrained.

Exp. 17. June 2, 1:30 p. m. Temperature, 66° F. If anyone should offer the criticism that my experiments were made early in the day, too soon after the moths had come in from their flight at dawn and their reactions were merely a result of the momentum acquired in that flight, or that some of them were made too late in the evening, at a time too near to the approach of their next flight at dawn, Exp. 17, which was made at 1:30 p. m., a time half-way between the two, should set them at ease.

Thirty-five males that had flown in at dawn were kept in the darkened glass box until 1:30, when they were all gently placed at the north end of the box and the curtain was lifted from the south end. They were so utterly lethargic that they seemed fast asleep. Since, as we know, insects do indulge in sleep, why should not this time of day be most suitable for them?

Within six minutes, however, six males were fluttering at the light end of the box, and during the next few minutes this

number increased to 17. At 1:50, after the light had been played upon them for twenty minutes, 25 moths were counted at the light side. When so many were moving together, it was hard to tell just how long each moth continued its activity, but in this experiment ten minutes seem to be the limit for any one individual. Thus we see 71 per cent of this population reacting to mild light rays at a time of day midway between the two normal periods of darkness.

Exp. 18. This is a continuation of Exp. 17, but made with a purpose of getting additional data on the reactions of moths to light of greater intensity.

These same moths, 35 in number, were placed at the south end of the cage and kept in darknesss for 25 minutes. Then the curtain was lifted and a 40-watt lamp was pressed against the glass at the north end. Now the intensity of the light from this lamp was intermediate between the two extremes previously used, a 75-watt mazda lamp and the subdued light of the room. This being the case, we should expect the number that respond to be intermediate between the numbers that reacted to the two extremes.

During the first five minutes, four moths flew to the lighted end, but after a few seconds three of them retired again to the dark side and one alone continued its activity. Ten minutes after the curtain was lifted, 8 were fluttering at the light; their movements gradually became less intense, while slowly a few others came, until at the end of 35 minutes, 12 were at rest at the light end of the cage. This is 33 per cent of the total, which responded to the light of a 40-watt lamp, while less than 8 per cent reacted to the strong light of a 75-watt lamp, and 71 per cent responded to the diffused or dim light of the room. How gratifying it is to find our anticipations fully realized; the proportion of moths responding to the light of intermediate intensity was just about midway between the proportion responding to either extreme of light! It is also evident that the time required to induce the reaction is increased with the intense direct light. In 20 minutes we got 25 males to fly at the stimulus of diffused daylight, whereas in the direct light of a 40-watt lamp it required 35 minutes to influence half that number. But best of all in this experiment, we prove that the hour of the day is no stimulus to action, but light conditions are, re-

gardless of whether the experiments are carried on morning, noon or night.

Exp. 19. This test was made to test the reaction of the female cecropias to light. In the literature one finds little or no mention of the activities of females, excepting their mating or egg-laying. People are satisfied with the assumption that the female merely sits and awaits the arrival of the male; hence it is startling as it is interesting to find, experimentally, that she sometimes plays an active part in the meeting of the sexes.

Thirty-two females, all from one lot of cocoons and all three days old, were placed in the dark box at 8 a. m. After 6½ hours the cover was lifted at one end and the six which chanced to be near that end were gently placed in the dark corner. Within five minutes seven of them had come to the light end; for a time two fluttered about excitedly, more actively than one would expect of a heavily laden female, but they soon subsided. Fifty minutes more were allowed, but no more responded to this stimulus. Then the light was changed to the 40-watt lamp with a reflector on the back, pressed against the end of the box. Only two more responded to this dazzling illumination by moving ten inches toward it; a half hour brought no further movements. Lastly, the entire cover was removed, admitting diffused light of the room from all sides, but not a moth stirred.

After a half-hour's rest I placed a cage containing seven two-day-old males in the box, at the end nearest the window, and fanned the air into circulation. Within ten minutes eight of the females had flown to this end of the box and three of them, heretofore sluggish or immovable, were clinging to the cage desperately beating their wings against the wire mesh. After fifteen minutes eleven females were around the cage of males, some of them in wild excitement.

These tests show, then, that some females at least (7 out of 32 in this case) mildly register the perception of light per se, but when the stimulant of sex odor plus movement of the air is added, a larger number (11 out of 32) show intense excitement and aggressive action. This experiment clearly shows, too, that not all of the females are similarly endowed for the perception of light or odor waves.

To conclude, then, with an answer to the query in our opening paragraph, we find that some females at least are endowed

with sensitiveness and react to certain conditions of light and odor; moreover, some display much emotion, and some make strenuous advances in courtship.

Summary

We find that the phenomenon of the nocturnal periodicity of the males is not so deeply ingrained in the psychology of the cecropia moth that it cannot be changed with changes in the condition of light and darkness. It seems they respond to re-recurring periods of light of certain intensity, whether these periods occur once or half a dozen times in the twenty-four hours. If the measured periods were deeply ingrained in their beings, whether physiological or psychological, they would react only when the cycle (hour) recurred, regardless of whether they were in a darkened box or in the brightest sunshine. As a matter of fact, they do not become active under either of these two extremes, but the optimum activity is reached under conditions of diffused daylight, which to them is probably similar to the light of very early dawn. If this condition is created at almost any time, a good percentage of responses may be expected.

In regard to the females, the experiments show that they respond mildly to proper light conditions, and more actively when the odor of males is added. The female is not wholly devoid of sex perception; she has the ability to perceive his odor and has the power to reach him when he is in the path of light. Moreover, she displays enough emotion to proclaim to the world that she, too, is a party in the courtship.

The results of this series of experiments on light reactions show for the males at least positive response to the stimulus of diffused daylight, negative response to direct electric light of high intensity, and a response half-way between the two for an electric light of medium intensity.* This, of course, is what one would expect in a moth whose activities are influenced by day-

*Kennedy (Ann. Ent. Soc. Amer. **20**: 87, 1927) finds that many nocturnal insects are so sensitive to light that they are thrown into a state of catalepsy in strong light by overstimulation. He found stone flies attracted to a 75-watt light half mile away, ignoring a 300-candle power gas mantle lantern on a creek bank. He also found may-flies hanging on a wall motionless, with an electric light on. The light went out and a single candle was lighted; some two dozen that had been hanging motionless then became fully active.

light intensities of the period of early dawn, when their normal flight takes place. In nature, bright light means enemies and danger if they are in flight; therefore daylight means motionless rest and sleep. The reactions which the moths displayed in our tests would be very fitting in the wilds of nature.

Activity in a Dark Room.

If the rhythmic periodicity is something innate and is not influenced by surroundings, then we shall find in these moths the activity returning with the recurring hour each night, regardlesss of external conditions. If we shut out the stimulus of light, by keeping the room entirely dark, we should expect to find that the flight has occurred at the regular time, and in the morning the moths will be scattered about the room. To this end the following experiments were done:

Exp. D16. June 4, 9 p. m. Fifty-two moths, comprising thirteen each of male cynthias, female cynthias, male cecropias and female cecropias, were placed on the south wall and the room darkened. The next morning I found 36 moths just where I had left them, and 16 were crowded around the door; this door was closed, but did not fit tightly at the bottom, and where a small pencil of light penetrated, the only streak of light in the room, they had congregated. This simple test shows that the moths do not act merely because it is their appointed hour to act, but without the stimulus of a precise condition of diffused light they pass the hour of dawn unmoved. It also shows that some supersensitive individuals can sense a meager trace of light and respond to it.

Exp. D17. May 5, 11 p. m. We know that polyphemus are abroad in quest of mates during the entire night, and that their activity is influenced by moonlight. In this experiment we want to see if they can be induced to inhibit their activity during the night if they are placed in a totally darkened room. If they fail to move about when the luminous rays are eliminated, then we know that the rays influence or perhaps induce the movement. If they react in spite of the absence of any variation in the light, then we shall feel that their reactions are innately bound up with the physiology of their beings and reappear at recurring periods, regardless of any outside stimuli; in other words, their rhythmic periodicity recurring once in each

twenty-four hour period, is as deeply rooted physiologically as the rhythmic periodicity of the mammalian heart-beat.

The room was darkened to the best of my ability; even the troublesome crack under the door was plugged. Twenty-eight polyphemus of both sexes were used; some of these were 2 to 5 days old, and had been used in previous experiments and had reacted to light stimuli, and some were young moths, ½ day or less, which had never had such an experience. All of the moths were placed on a blanket on the south wall and left undisturbed for the night.

At 7:30 next morning all of the moths were in their places; a few of the energetic ones had crept up the wall a few inches, but among the older ones not one had moved at all. A second examination at 7:45 p. m. showed that there had been no flight during the day. Some had crept up the wall a few inches more, and a few had fallen to the floor, but lay just beneath the blanket. Thus it was evident that they had not at any time in the twenty-four hour period been overtaken by the wild paroxysms of excitement and flight that they display out under the stars every night, or they would have been scattered all over the room. Even though the 14 older ones had during the last three or four days flown repeatedly to the window in other experiments, not one of them now so much as started toward the same window, either by day or night, when the light was excluded. At 9 p. m. there had been no movement, so the experiment was changed.

At the opposite (north) end of the room was a closet with a drop electric light. Here a 60-watt lamp was turned on and the door almost closed, so that only a pencil of light one-fourth inch wide and as high as the door shone out. Between 9 p. m. and midnight, 7 moths came to this light (3 males and 4 females), and the next morning 6 more were there. These 13 included both young and old of both sexes. When I examined those which did not respond, I found 10 dead in their tracks and 5 aged females; hence there is evident reason why more did not react.

Thus this simple test shows that these polyphemus do not act merely with the recurrence of a certain interval, but they must have light rays (of a low intensity), of course, to stimulate or enable them to go through the usual activity. This

leads to the conclusion that their movements are caused by external stimuli and not by something within.

Relation of the Movement of Male Cecropia and Polyphemus to Moonlight.

While waiting through the night hours for the moths to come in, it often seemed to me that on moonlit nights an unusual number of moths were abroad. To test this point, I remained on watch all night, or all but an hour, for seven nights, and kept records of the moths appearing on the roof, together with the weather and moon-light conditions at the various times. The resulting data are too bulky to be presented here, but the following table gives a summary of the seven nights' observations:

	No moonlight	Bright moonlight	Half moonlight	Dense fog	Total
Bred cecropias	5	3, 14, 8, 5	1, 12	0	48
Wild cecropias	0	2, 0, 0, 4	0, 1	0	7
Bred polyphemus	1	1, 3, 7, 1	1, 0	0	14
Wild polyphemus	2	4, 0, 29, 5	0, 4	0	44
Total number flights	8	86	19	0	113

Immediately the figures show that my impressions were not in error; the average number in flight on the bright nights was more than twice the number on dark nights. The times when the moonlight was subdued or when light and darkness fitfully alternated brought forth an intermediate number of moths. It is easy to imagine that they awoke and started on their journey during an interval of brightness, and the temporary darkness did not arrest them. On one night the moon was completely obscured by a dense fog, and all night long I waited in vain, for not a single moth of any description came in. I cannot believe that the severity of the weather, the difficulty of flying in the moist atmosphere, could have prevented their flight, since I have seen them come in in large numbers through a drenching rain. Rather, this instance may be explained by the lack of wind. Our previous evidence indicates that wind is the chief factor in inducing the flight of moths in the open, and fog indicates a total absence of wind; hence the moths could

not orient themselves to the cages on our roof. Of course it is possible that the faint light might have aroused them to action, and that they were flying aimlessly hither and thither, without any trail to follow, and we could not know this. Thus it is evident beyond doubt that moonlight is a potent factor in the activity of these creatures, arousing them to action in a considerable number of cases at all hours between 11 p. m. and the hour of dawn or 3:30.

The species also vary in their response to moonlight. During these seven nights the wild cecropias came in at dawn in hordes, but only 7 responded to the moonlight at other hours, and none at all came in early without moonlight. The cecropias which had emerged from cocoons kept in the laboratory showed a far greater tendency to fly by night, not waiting for dawn as had the wild ones. Although the wild ones in the region far outnumbered the bred ones which we had liberated, yet 48 of the bred ones came in early as contrasted with only 7 of the wild ones.

The polyphemus shows a much stronger tendency to fly at all hours of the night instead of confining their activity to the hour of dawn. Although they are not nearly so numerous as are the cecropias in this region, they came during the moonlight (table above) in equal numbers. The figures above indicate that polyphemus is more susceptible to moonlight.

Thermotropism.

On May 16 at 8 p. m., I had 20 male cecropias and 3 male polyphemus in the glass box. The temperature was low (54), and they did not respond readily to my light experiments, for only 4 moved. Therefore I placed an electric heater in the box and watched the thermometer go from 54 to 60. This brought an additional 6 to the light side. When the heater was turned off, they rested. An hour later the heat was again turned on and the thermometer reached 64. One by one the moths which were already at the light side of the box resumed their agitation, and were joined by ten others which had remained indifferent to all stimuli at a lower temperature, until soon all in the box were active. Now this temperature is not high for these species, for in Nature, during the period of their adult life the temperature is often above 80. The reaction is to be explained

as one of differential sensitivity; the change from 54 to 64 aroused them to a response to the light. The heater was turned off; a half-hour later the thermometer still registered 64. The light end of the glass box was gently darkened, and the cover lifted at the opposite end admitting the light. Within four minutes 10 cecropias and 2 polyphemus (more than half of the lot) had traveled to the light side.

On May 4 the temperature of the room was 59; this was lower than that of the three previous days, which had been 71, 66 and 68. The moths in their cages were very sluggish; none would move about unless prodded. These were 9 in number, 2 male and 3 female polyphemus and 4 male cecropias. At 9 p. m. I placed an electric heater so that a stream of heat waves would pass through all of the cages. Almost immediately they began to "come to life," and soon all were fluttering about the tops of their cages. There was only one exception; that was a female polyphemus only six hours old. When at last the thermometer among the cages registered 80, she also became active, but moved downward. Thus it is apparent that a sudden rise in temperature is conducive to the activity of these creatures, whereas at a lower temperature they remain motionless. The only thing that puzzles me in this matter is the question of just how this factor would function in the lives of the wild moths. All marked rises in temperature are very sure to occur during the day, at which time they are never abroad; hence it seems to me there would always be a conflict of reactions, whether they should respond to sunlight by sleeping or respond to rising temperature by waking.

Normal Activity.

I have shown in the electric fan experiments how the occupants of a cage in close proximity to another cage wherein the moths were in a high state of activity were not susceptible to suggestion, and remained uninfluenced by the activity of their neighbors. In other words, despite the fact that the males could see, smell and hear the activity of others near them, they offered no imitation. The moths became active only when, in the language of the street, "they got good and ready." Of course that means when their physiology became attuned to something or

other. The following data, gathered at odd times among other tests, substantiate the electric fan experiments.

On the evening of May 5 the temperature was from 58 to 64 F. There were four males (polyphemus) in separate cages and 5 females in another cage side by side on the table. No contrivances for artificial wind, heating or lighting were used, excepting the ordinary electric lighting which illuminated the whole room. I merely watched to see if any of them seemed to be influenced by the activity of one, or to imitate it. Now when the males become active in these screen-wire cages, the vibration of the wings against the mesh creates a humming which is almost musical, and loud enough to be heard from the floor below; the motion of their wings can certainly be seen by their near neighbors, it is probable that the motion of the air thus caused could be felt for a short distance, and lastly, the beating of the wings must stir up and disseminate the odor from their bodies which the others should be able to perceive. In short, it seems reasonable to think that one of these moths might become aware of his neighbor's activity through sound, sight, odor or touch.

Male 5, age 2 days, became active at 8:00 p. m.
Male 4, age 2 days, became active at 9:10 p. m.
Male 2, age 5 days, became active at 11:05 p. m.
Male 3, age 5 days, became active at 11:30 p. m.

Each of these remained active for five to ten minutes, and then stopped. Thus each conducted his own affairs without the slightest consideration of the dictum "everybody's doing it." The five females in an adjacent cage showed no response whatever.

One sees much variation in the duration and strength of the activity of the individuals in their cages. The activity of groups is in great measure regulated by weather conditions. Cool periods, especially in the early months, cause long periods of lethargy, while warm days call forth periods of activity. It is not surprising that the females are much less active than the males, in both frequency and strength of movement. For two weeks I made careful note of two polyphemus females, and found them almost never moving from the very spot where they were placed on the wires, where they clung with great tenacity. Dur-

ing a period of two weeks there was never a voluntary movement. I think this unusual lethargy may be attributed to the low temperature of that time. The minimum for the fourteen days varied from 38 to 64 F. When a female was handled or prodded, it slowly opened and closed the wings, and lapsed again into repose.

One evening from 10:30 until midnight I permitted a very lively male to flutter about the room, and soon he turned his attention to the ten cages containing 18 females. The position of each of the moths was marked with paint on the outside of the cage. As his flutterings among them became more and more wild, I expected some sort of response, at least a movement of the wings, but not one of them stirred during the hour and a half, and the marks at the end of the time showed that no unnoticed movement had occurred. The temperature was 55. This temperature did not cool the ardor of the energetic male, but the females were indifferent in his presence when the temperature was below optimum. On other similar occasions, when this factor was favorable, the females have displayed emotion. On May 18, when the temperature was 75, one female which had just concluded mating fluttered at intervals for six hours.

Rythmic Periodicity in *Platysamia cynthia.*

Cynthias are sluggish in cages and are seldom seen to move. They are good fliers, however, and in moving them from cage to cage one must be careful, for they are quick to escape, and once out of the window they fly high, even when the sun is bright. But they do not like the sun, for they always come to rest in some shady spot. The females often remain motionless for days at a time, but if one is liberated in the open it flies high and more lightly and swiftly than cecropia.

We have seen in the cecropia that light of the optimum intensity at any time of day regulates the activity of the males and to a lesser degree that of the females. In nature, the normal time for the flight of cecropias is just before and during the hour of dawn; it seems that some of the males can perceive the approaching dawn and fly before dawn overtakes them. Under very exceptional circumstances, cecropias fly at other hours during the night, as noted in the early experiments on homing. The time of flight of cynthias is several hours before midnight. They present a distracting list of variations in their flight; sometimes

male cynthias fly in at dawn just as cecropias do, and others even when liberated near the windows where the females are, wait until dawn to come in; on moonlight nights they respond to some extent to the light of the moon, and they never fly by day, although Weed* states that on cloudy days they fly during the day. All this, though confusing, indicates that the flight of cynthias is regulated by light conditions and that in the evening at certain periods and at dawn the light intensities are such as to cause response. This, of course, means that cynthia finds more periods out of the twenty-four hours when light conditions are optimum for its activity, whereas cecropia under natural outdoor conditions reacts during a very limited period of one hour during dawn. Since cecropia with its usual limited period for response reacts to light conditions (experimental) at any time during the twenty-four hours, what must we expect under experimental conditions for cynthia, which has been found active at various times of evening, dawn, night and even cloudy days? In the face of these difficulties, experiments were undertaken to see what their reaction would be to definite light conditions. Since the glass box was then in use for the cecropia experiments, the following tests were made in the third-floor room with two east windows. The following year two box experiments were made, and these are given first.

Exp. 20. June 23, 1924. At 7 p. m., five cynthia moths (3 females and 2 males) were placed in the glass box and this was completely darkened and kept so for thirty hours. At 1 p. m. the next day, the cover at one end was lifted, but none flew to the light then. When I examined the box at 6:30, none had gone to the light, but at 7:30, all had flown to the light end of the box. This indicates, of course, that they are not influenced to activity by conditions of light or darkness, but that their activity occurs periodically.

Exp. 21. June 6, 1924. At 7 a. m., twelve cynthias of both sexes were placed in the darkened glass box, with the cover lifted at the north end. They were given an opportunity during the entire day to move to the light, but up to 7 o'clock all remained precisely where they had been placed. Between 7:15 and 8:05, all but one flew to the light. At this time six more of both sexes were added at the light end of the box and the cover

* Butterflies Worth Knowing, p. 14, 1917.

dropped, and the light was admitted now from the opposite end. There were now 18 moths in the box. By 8:15, two were at the light, at 8:45, six and by 10 p. m., twelve were at the light end. During the night the others followed, so by day-break all were there. This of course was their normal period of flight.

All of the 18 were left there, and the lighting was again reversed by dropping the cover and raising it at the opposite end. This was done to see if they would travel to the light during the day. Up to 6 p. m., only three had moved to the light, but at that time the migration seemed to occur, for by 8 o'clock six more were there, and at 10:30, sixteen were there and the other two were dead, so the result may be considered 100 per cent. At 11 p. m. the curtain was again dropped over the end where they were congregated and lifted at the opposite end. No detailed observations could be made during the night, but the next morning at 6, all were again at the light end.

Exp. 22. June 26, 1923. At 8 p. m., six cynthias which had emerged during the day were at rest on the south wall. Eighteen males which had successfully made a flight to the roof two nights before were placed on the north wall. Then I shaded a 60-watt lamp which hung in the middle of the room in such a way that the six moths were brilliantly lighted, and the wall with the 18 males was dimly lighted. This arrangement was left from 8 to 10 p. m., but it gave rise to no response in either direction, either toward the bright light or to the subdued light. Then I reversed the illumination, throwing the six in the dim and the eighteen in the strong light. During the next two hours there was no response from either group of moths.

Before retiring, I placed whatever cynthia material I had on hand on the south wall, and left the room darkened excepting the light from the street which entered a small window with the shade half drawn near the north end. There were now 82 moths, of which 54 were males and 28 females. At 3 a. m., none of them had moved. I was not on hand at sunrise, but a little later I found great numbers of the moths at or near the window; on the window and sash were 46 males and one female; on the walls near-by were 7 males and 7 females, making a total of 60. When a census was taken of those which had made no attempt to come to the light, there were 21 females and one male!

Thus we see that practically all of the males moved to the

light, and about one-fourth of the females also. In all probability these cynthias did respond to the light of early dawn, because in the homing experiments many of them did come in with the cecropias at about 4 a. m. In this case, as in the other species, it is surprising that the moths did not respond to the glare of the automobile headlights flashing intermittently in the windows before the hour of 3 when I examined them.

In the first part of the experiment there was no reaction to the intense light, because physiologically they were not attuned to become active in those conditions, but later experiments will show that even when the hour recurs for their activity, they will not react if the stimulus of correct light is lacking. It is interesting to note that, when once they are in the light, there they remain quietly at rest throughout the day, regardless of the fact that the hot sun is curtailing their lives*; they have never been observed to make the slightest move to seek a more sheltered place. When once in the light they seem to be trapped. During these periods they cling tenaceously to their support; unless one has the task of pulling them off, one little suspects that their feeble-looking tarsi possess so much power. With the return of night, they fly wildly about the window pane.

In this experiment where all of the males and 25 per cent of the females went to the light, one would expect all of the females to have mated; on the contrary, only one pair mated, even in this close proximity. In this species as in the cecropia, the purpose of the action is to fly to the females, and the stimulus is light rays of a certain intensity, but in the excitement of the reaction or for some unkown cause, they pass by the females even when in close proximity and the vital purpose is defeated. Someone may stretch a point to say that the passing by of the males when too near to the females may be an adaptation to insure cross fertilization, since probably all the adults of a limited area are from the eggs of one mother. But who, pray tell me, would be so bold as to make a case of this speculation? It is much more likely that there was no mating at the window because there was no motion of the air.

Exp. 23. June 27, 11:50 p. m. Room dark; only three-quarters of one window in the northeast corner uncovered; no wind

*In the case of an insect that takes no food, the duration of life is shortened by warmth and lengthened by coolness. See Rau, Trans. Acad. Sci., St. Louis, 23:1-78, in 1914.

in room. Fifty-three males were placed on the south wall, and on the floor a few feet in front of them was placed a cage containing 40 females. The object was to see if they would be attracted to the females in preference to the rays of light at dawn, despite the fact that the air was motionless.

Heavy rain and wind prevailed during the night, and at 5 a. m. when I went to the room I found a cool, gray dawn, with less light than usual at that hour, but at the lighted window were 48 males; only 5 remained unmoved. All of these had passed by the cage of females, but not one had paused in his response to the lure of the soft light of dawn. But furthermore, I had placed at the window 10 females without a cage, but despite the fact that there were here five males to each female and in close proximity, there was not a single case of mating among them.

I left them there and could pay no attention to them until evening. The sun shone intermittently during the day, and at times they were in the hot June sun, but none retreated to more comfortable quarters. During the evening, I watched them at short intervals to see at what hour their activity would begin. Until 8:30, all were quiet, but at 9 o'clock I found about half of the males fluttering wildly against the pane, as if they were trying to reach the moon, which was by this time shining in front of them. It seems that this action was actually influenced by the bright moonlight, for only ten minutes later when the moon was suddenly hidden by a cloud, all but two of the moths as suddenly ceased their activity. All this time the two cages of females, one with 50 that were four days old and the other with 40 moths 1½ days old, were in the room, about ten feet away, but not one male showed the least indication of leaving the lighted window to pay them the slightest heed. This startling condition cannot be without significance in determining the senses of these creatures. Lutz,* in referring to the case of moths where the males are supposed to locate the females by odor, says: "that none of the experiments believed to have demonstrated that odor is the guiding factor in the case of moths have absolutely ruled out sound, and male moths have antennas quite as plumose, apparently as well fitted to receive sounds, as those of male mosquitoes." This statement, of course, pre-

*Insect Sounds. Am. Mus. Nat. Hist. 50:337. 1924.

supposes that the sounds must be emitted by the female, if the male is equipped for hearing such sounds. Here in two cages were 90 females of attractive ages at one end of the room, and if they had emitted a sound which the males could hear, surely at least one out of the 48 which were at liberty in the same room should have responded.

After the moon had reappeared and the moths had resumed their fluttering against the pane, I turned on the 50-watt lamp in the middle of the room to find if, while they were in this state of excitement, their attention could be directed from the moonlit window to the bright light near by. It will be remembered that in Exp. 22, when the moths were quiet, there was no reaction to this type of test. After 30 minutes, 23 of these, or about half the number, were flying vigorously about the room.

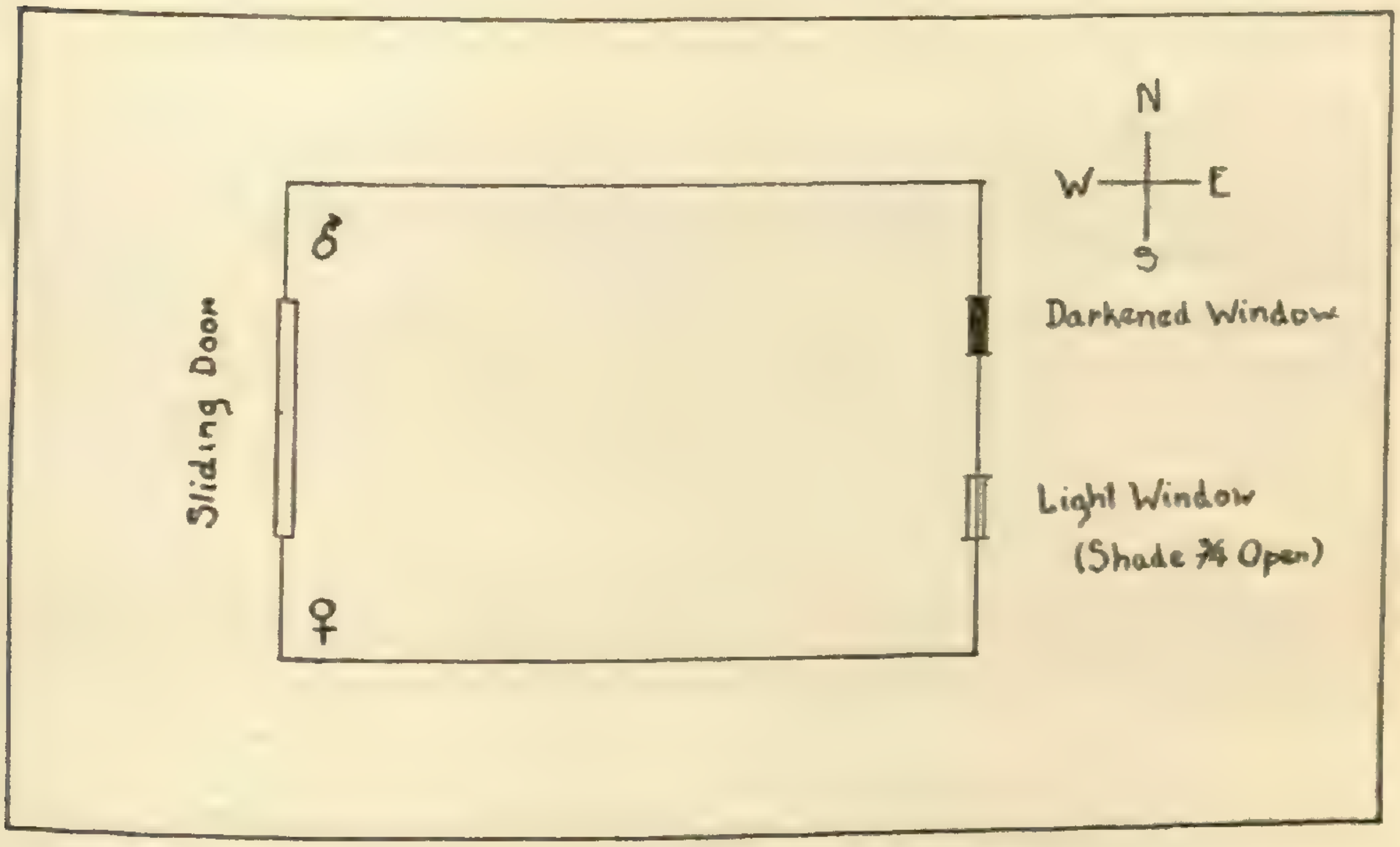
At 10 p. m. the room was darkened and all of the males, now 47 in number, and 10 females were placed on the south wall. At 3:25 I awoke, early enough I thought to observe the migration, but I was mistaken, for already 43 males were resting on the window sash at the northeast corner of the room. Whether they had responded to the lure of the moonlight during the night, or whether they had been guided by an impulse to move at the accustomed hour, I do not know, but at that time the moon was low in the west, while the window faced the east.

At 9 a. m., there was no change in their positions, so all were replaced on the south wall, to see if they would react to the lighted window in the same way during the day. They were watched at frequent intervals, but not one moved to the window during daylight hours. Between 8 and 9 p. m., however, there was a general exodus, 40 males and 3 females making their way to the window at that time. The moon could not have caused the exodus, for it did not rise until 9:30. I have wondered what part the flashing headlights of automobiles, as they came out the park gate opposite, might have had to do with their action after dark.

At 11:05 the old and decrepit males were eliminated, thus reducing the number to 27. These were again placed on the dark south wall. The next morning, all but 3 were again at the window. It had been my intention to take a nap until two o'clock and then watch them constantly until dawn, to get the actual time of their movement, but the weakness of flesh prevailed, and

I missed this observation, so this night means but little. In the morning I once more placed them on the south wall, to see if they would respond to the light of the window during the day. This test, with identical surroundings and material, had previously given negative results during daylight hours. This time, however, there was some reaction, which shows that the moths can as they grow older, or through place memory, create new periods of activity. Before noon six of the males, almost one-fourth of them, had flown to the lighted window. These moths, remember, were the identical ones which had declined to do this trick for us on previous days, under conditions which were, so far as we could see, identical.

These six were replaced on the wall. At 8:30, I found them all fluttering about the room; 9 went to the window during my five-minute visit, but I could not remain with them. At 11 p. m., 25 of the 28 males were on the window. The moon did not appear until 9:15.



Exp. 24. June 28, 9:55 p. m. This experiment was arranged as indicated in the diagram above. All of the moths were ½ day old, 28 males were placed in the northwest corner and 28 females in the southwest corner of the room. One window on the east was darkened, and the other had the shade lifted four feet. The objects were to see:

(a) If both sexes would go to the light;

(b) if one or the other sex would cross over and reach the opposite sex instead of following the light.

(c) if these moths would react in the same way to this arrangement of stimuli on successive days and nights, i. e., as their age and experience advanced.

An examination at 3:30 a. m. revealed that 14 males, exactly one-half, had travelled to the lighted window, diagonally across the room from where they had been placed, and one had gone along the wall to the adjacent corner and mated with one of the females. Not one of the females had moved from where I had placed them. At 8 o'clock the next day examination showed all of the males (excepting the one in copulo) at the lighted window, in the bright sunshine. None of the 28 females had reached the light; only four had attempted to do so, but had traveled only, 1, 2, 3, and 5 feet. This window faced the street with automobile lights also.

At 9:15 a. m. all the moths were placed in their original positions on the wall; 8 returned to the window before noon. It seems that they were now breaking down some of their stiff instincts by responding to lights at periods that differed from the set rule. These moths were in prime condition, a little more than one day old, when 8 out of 28 moved to the light in midday. If this reaction to light of this intensity is truly phototropic, we should rightfully expect to see all of them respond in the same way, just as they all did to the rays of dawn in the previous tests. In Exp. 21, the six males that responded to the light during the day were much older than these and, since they had failed to do so before, I attributed their reaction to their age and experience. The fact that these younger ones behaved similarly immediately thereafter leads one to wonder if there might be something in the season or the light conditions of these late June days which modified their action.

At noon all of the males were returned to their original places; I then had to leave them until 9 p. m. At that time all of the males were again on the window and 15 of the 28 females were on the sash or near it.

Exp. 25. June 29, 10 p. m. This is a continuation of the last experiment, with the same room arrangement, but in addition to the 28 males and 28 females, 53 females were also placed at the southeast corner of the room. These 109 moths included: 28

males 1½ days old, 13 females ½ day old, 28 females 1½ days old, 20 females 2 days old, and 20 females 5 days old. The moths of each lot were given a distinguishing mark for their identification. The object of this experiment was to see at what age the females were more likely to be influenced by the light of the uncovered window. The males were retained in the room to serve as a check. At 8 a. m. next morning, all of the males were at the window, and the following females:

Age, days.	Number used.	Number attracted to light.	Per cent attracted to light.
½	13	0	0
1½	28	18	64
2	20	16	80
5	20	17	85

This shows most remarkably that age is a factor in the activity of the females; the figures in the per cents column speak more distinctly than words.

At 9 a. m. the moths were replaced in their respective corners; they were all, of course, a half-day old in this test. Up to noon, 3 males (2 of which had made two flights and 1 had made one flight previously) moved to the window; these were replaced and the experiment left alone until evening. At 9 o'clock, the census revealed that all of the males were again at the window, fluttering excitedly about the pane. Of the 81 heavily laden females, 62 had left the wall in their respective corners and were making their way slowly eastward, vibrating the wings intensely as they crept, as though being slowly but irresistibly lured or even dragged across the floor toward the light. Only 3 had actually reached the goal, and were climbing to the frame. The females were of all ages as follows:

Age, days.	Number used.	Number attracted to light.	Per cent attracted to light.
1	13	7	54
2	28	24	85
2½	20	17	85
5½	20	14	70

Here is more evidence of delightful clearness; the moths which, when half a day younger, remained indifferent, now under identical surroundings, respond to the extent of 54 per cent of their number, to the light stimulus. The second group, those now two days old, had increased their efficiency from 64 to 85 per cent; the third group, still in their prime, improved upon their old record only slightly, while the oldest, now verging on senescense, were beginning to wane. During the night 3 more females became travellers, and next morning three pairs of the moths were in copulo on the window sill. Unfortunately, I did not ascertain whether the air in the room was in motion.

Exp. 26. June 29, 10:45 p. m. In the previous experiment, we found the males going to the window and the females following, but after all we do not know whether the latter responded to the light rays or followed the odor trail to the males. For this reason we wished to repeat this test in a room where no males were present, and to make the conclusions absolute, in a room where there was no possibility of male odors lingering about the windows. Therefore the family meekly submitted to ejection from still another room in the house, this time the living-room, which was transformed into an improvised laboratory. All windows were darkened excepting one in the southeast corner, likewise facing east, and 54 moths were placed on the wall in the northwest corner. There were 13 females ½ day old, 5 were one day, 17 were 2 days and 19 were 5 days of age. All were marked and placed on the wall at 10:45 p. m.

The next morning revealed but slight activity during the night; only two moths (aged 2 and 5 days) had reached the window, three had moved about a foot toward it, and about a dozen had crept upward a few inches on the wall. This seems, when compared with the previous test, a rather discouraging result. However, one must not lose sight of the fact that the others had rested all day and had done practically all of their moving between 8 and 9 o'clock, while these had not even been placed on the wall until after that hour.

At 9 a. m., all were replaced on the wall, but none moved to the light during the day. Between 8 and 9 p. m., their customary hour, their agitation began; 43 moved all or part way to the window; only 11 remained on the wall, and these moved slightly. Of course they were now one day older than recorded

above. Eventually all of the travelers reached the window or sash. Unfortunately the actual numbers in each class were lost, but all groups were represented, while in each group were from 1 to 4 which failed to respond. The experiment adequately demonstrated that in a room without males or the possible odor of them, the females react to the light just the same as if the males were there; hence the light per se is the stimulus.

Exp. 27. July 1. This was to be the final experiment of the season, so I took all the cynthia moths that I had on hand and placed them on the south wall of the third-floor laboratory. The light was admitted at only one window. I merely wanted to see how the moths of various ages, sexes and conditions would respond to the lure of the light. The lot consisted of:

Normal moths: 8 females 2 days old, 6 females of unknown age, 6 males 2 days old, 17 males 4 days old.

Moths with right antenna off: 3 females, 4 days old, 6 females 7 days old.

Moths with left antenna off: 5 females 2 days old, 3 females 4 days old.

Moths with both antennae off: 10 females 2 days old, 4 females 4 days old.

Moths with half of each antenna off: 2 females 2 days old, 3 females 4 days old, 5 females 7 days old.

Moths with paint-covered eyes: 7 males ½ day old, 13 males 2 days old, 7 males 3 days old, 15 females of unknown age, 13 females 3 days old.

These 133 marked moths were placed on the wall at 4:30 p. m., in time for them to become composed before their evening hour of activity.

By 6:45 p. m., 22 moths (10 males and 12 females) were on the window; 6 of these were normal and 16 were mutilated, and in the lot were 2 blind males only ½ day old, for whom this was the first night in this world, and 2 other blind males 3 days old, which of course had experienced twilight previously. These 22 which responded about two hours earlier than their usual period of activity constituted about 17 per cent of the total population under experimentation. This test shows also that the moths are able to make the flight under the handicaps mentioned above. In the entire lot 72 per cent were handicapped,

and among those accomplishing this early flight 73 per cent were thus modified.

These 22 venturesome moths were put in a cage until I could return to them. At 7:30 I opened this cage and stationed myself to observe the conduct of the entire group during their busy hour. Within 15 minutes, 10 of them had succeeded in making their way to the window; at 7:52, when the last gleams of daylight were leaving the sky, 21 moths were fluttering about the window. During the next 3 minutes, 9 more joined them. At about this rate, more and more of them joined in the migration, until about 9 o'clock, when the excitement began to wane. At that time 66 were there, or about one-half of the population. The moon did not rise until 10:30. A census at 11 p. m. gave the following data:

TABLE No. 6.

	No. In Exp.	No. that Responded	Per Cent
Class:			
Normal females	14	4	28
Normal males	23	22	96
Females, right antenna off, 7 days	6	0	0
Females, right antenna off, 4 days	3	0	0
Females, left antenna off, 2 days	5	5	100
Females, left antenna off, 4 days	3	3	100
Females, all antennæ off, 2 days	10	5	50
Females, all antennæ off, 4 days	4	0	0
Females, ½ both antennæ off, 7 days	5	5	100
Females, ½ both antennæ off, 4 days	3	3	100
Females, ½ both antennæ off, 2 days	2	2	100
Males, blind ½ day	7	5	71
Males, blind, 2 days	13	8	61
Males, blind, 3 days	7	2	28
Females, blind, 3 days	13	1	8
Females, blind, 7 days	15	1	7
Summary of Table:			
Normal moths	37	26	70
All moths, right antenna off	9	0	0
Females, left antenna off, all ages	8	8	100
Females, all antennæ off, all ages	14	5	36
Females, ½ both antennæ off, all ages	10	10	100
Males, blind, all ages	27	15	55
Females, blind, all ages	28	2	7

The summary of the data gives some highly interesting evidence. Of course the numbers are too small to be accorded much serious consideration, but nevertheless they are very interesting indicators. It appears at first as an unusual case of accident or chance that all moths with the right antenna off failed to come to the window, while all moths of all ages with the left one amputated, succeeded. However, these results conform nicely to the results of Loeb's experiments with certain insects with anten-

nae removed. If the left antenna is removed, the insect moves in a circular direction to the right, and if the right one is removed, it turns to the left. Now the light came in at the window from the right of the insects' position, and all of them lacking the left antenna moved toward the right into the influence of the light, while those lacking the right antenna did not drift into the path of light and hence did not succeed. Of the moths (all females) with both antennae entirely removed, one-third came to the light; this is as good a record as any group of able-bodied females has ever made for us. This clearly indicates that when the female does come to the light she receives the stimulus through some organ other than the antennae, although if, through mutilation, they are unequal, she may be unable correctly to orient herself in making the journey. It is unfortunate that the lateness of the season prevented our having at hand enough males also to thoroughly test this question, but it seemed better to keep an adequate supply of them unmodified to serve as a check. This they did very well, responding to the light to the extent of 96 per cent of their number, thus proving that the conditions of the experiment were not at fault.

The case of the ten females from 2 to 7 days old, with one-half of each antenna amputated, is the most perplexing. Since females seldom respond to the light to a greater extent than 25 per cent, I cannot explain why these should have made 100 per cent response, except by mere meaningless chance or by some intricate arrangement of sense-organs in the basal portion of the antenna which we have not yet even suspected.

The moths with paint-covered eyes made far better returns than had been expected; 55 per cent of the males and 7 per cent of the females found their way to the light.

The puzzle remains, what combination of sensory responses in relation to environment really brings the sexes together? We see the males leaving the females and going to the light, there to find their mates, but evidently not following the odor and thereby arriving at the light. In this group, since there is so much greater response to light when the antennae are mutilated than when they are normal, it seems that normally the perception of stimuli, either odor or light or both at the same time, creates a conflict of feelings in the creatures. If the antennae, the organs of perception, are removed, then there follows a

stronger response to light, because odor is ruled out; if the eyes are blackened so that light is excluded, one ought to get better response to odor stimuli. The lack of material at the end of the season prevented me from putting this point to test. This could be done by blowing a stream of odor from one sex upon the other and when the insect is thus aroused, see whether it follows the odor trail to the source or flies away to the light instead.

In the blind tests, without the artificial currents of air, the response to the light was surprisingly high, but this may have been due to faulty technique. When the moths were examined later, a few tiny cracks were perceptible in the hard paint on the eyes; this may have been sufficient to admit enough light to guide them in their flight.

McIndoo insists that the olfactory organs are not situated in the antennae.

If we remove the antennae of males or females, and get better reactions to light because they can perceive no odors, and if then we blind others and get better olfactory responses because they are not distracted by light, would not that show the seat of the olfactory sense?

Experiments on *Cecropia* and *Polyphemus* in Reaction to Light.

It seemed to me that if phototropism were the cause of the reaction of these moths to the light, we should find all of the moths of one age responding at the same time, and if after they had flown to the lighted area they were immediately replaced they would again react in unison, so that when the experiment ended, all would have made the same number of trips to the light. With this in mind, I planned experiments with the following technique.

A room, 15 by 10 feet, had a small, uncovered window at one end; the opposite end was dimly lighted, closely resembling twilight. At this dark end, a blanket was tacked to the wall, to give a comfortable foothold to the moths. The insects were placed on this at the beginning of the experiment, and as soon

EXPERIMENT A

TABLE No. 7

NORMAL CECROPIA, MALES

Experiments Commenced May 29, 6:30 A. M., Ended May 31, 7 P. M.

Male No.	Age Days	Date and Temperature						Number of Responses	Remarks
		5–29 64–68 °F		5–30 60–68 °F		5–31			
		A. M.	P. M.	A. M.	P. M.*	A. M.**	P. M.		
557	1	7					7	2	
558	1	7, 8	7½, 9½	4½	1, 1½, 2, 9	7	7	11	
505	3		7½	4½		7	7	4	
507	3		6½, 7½		1, 1½	7		5	
509	3	8, 10	7½	4½, 11½	9	7	7	8	
512	3	8, 9, 10	6½	4½	1	7		7	
513	3	7, 11½	6½	4½				4	
514	3	7	6½	4½	1, 9	7		6	
511	3	8, 9	2, 5½, 6½	4½	9	7		8	
454	6	7	2, 5½, 7½					4	
456	6	10			9			2	
457	6	7, 8, 9, 10	2, 5½, 6½, 11	8				9	
458	6	7, 8, 9	7½	4½	1, 11½	7		8	
445	7	7	7½					2	
451	7	7, 8, 11½	2, 5½, 7½	8	1, 9	7		10	16 ♂'s made 97 flights or 6⅛ flights per male with a temperature of 60 to 68 °F.
442	7	7, 11½	5½, 6½, 9½		2, 9			7	
Total								97	

*At 11:30 all were placed on wall. No observation made until 7:00 A. M. next morning.
**All moths at window replaced at 7:00 A. M. No observation made between 11:30 A. M. and 6:45 P. M.

EXPERIMENT B

TABLE No. 8

Experiments Commenced June 3, 9:30 P. M., Ended June 6, 7:00 A. M.

Male No.	Age Days	6–3 68–70 °F	6–4 70–80 °F		6–5 70–80 °F		6–6 70–80 °F		Number of Responses	Remarks
		P. M.	A. M.	P. M.*	A. M.**	P. M.	A. M.	P. M.		
25	½	10½	3½, 8½, 9	3, 5½, 8..		7½, 9, 11, 11¾	7		12	
27	½	9¾	3½	8		6¾, 7½	7		6	
19	½		3½, 9		7½		7		4	
22	½		3½, 9	8		7½, 9	7		6	
23	½	9½	3½, 9			11			4	
25½	½		8½, 9	8	11½	7½, 9, 11	7		8	
30	1	9¾, 10¾	3½						3	
31	1	9¾	3½, 8½, 9	8		Died			5	
42	1			8	11½	6¾, 7½	7		5	
36	2	10¾	3½			7½, 11	2¾, 7		6	
37	2		3½			Dead			1	
40	2						2¾		1	
45	2		3½, 8½, 9, 11	5½, 8	11½	6¾, 7½	2½, 7		11	
46	2		3½	8		9	2¾		4	
48	2					6¾, 7½, 9	2¾, 7		5	
49	2				10	7½	7		3	
43	4		3½	5½			7		3	17 ♂'s made 87 flights or 5 2/17 flights per ♂ with temperature of 70–80 °F.
Total..									87	

*At 11:30 all were replaced on wall. No observation made until 7:00 A. M. next morning.
**All moths at window replaced at 7:00 A. M. No observation made between 11:30 A. M. and 6:45 P. M.

as they had flown to the lighted area each was immediately replaced on the blanket.

The experiments A and B, recorded in Tables 7 and 8 for male cecropia moths show that males do not react similarly or simultaneously or an equal number of times, although conditions and handlings were maintained as nearly uniform as possible. The column of totals reveals that the number of flights varied from 1 to 12, but there was no relation between the age of the individuals and the number of flights accomplished; moths young and old made both few and many flights. It is especially interesting, however, that all of the 33 males gave at least one reaction.

During the daylight series of experiments (A), begun at 6:30 a. m., some individuals reacted to the light within a half-hour, others were indifferent for varying lengths of time up to 13 hours. During the second series (B), begun in the evening, the first ones responded within a few minutes, while others were motionless for 3, 6, 12 or even 45 and 53 hours, before finally they were aroused and flew to the light. Not only was there great variation in the delay before their first flight, but even after the moths had once been aroused to action there was equally marked variation in the interval between their flights.

It seems that if the definition of tropism actually is "a form of externally induced behavior in which the organism automatically so adjusts itself as to have morphologically symmetrical portions equally stimulated," then why does not this external inducement treat all of the organisms that come under its influence alike, when age and conditions are alike?

The foregoing data were for the cecropia males. Tables 9 and 10 give the results of similar tests of the females, at the same time and conditions.

In the group of males, every individual in the lot responded to the call of the light (Tables 8 and 9). Among the females, there were five individuals which made absolutely no response during the entire period of experimentation. It happens that all of these were among the first lot, which were tested while the temperature was 64 to 68 F. Among those which were tested while the temperature was 70 to 80, every one of the females responded. Moreover, the latter averaged 4½ flights

EXPERIMENT C

TABLE 9

NORMAL CECROPIA, FEMALES

Experiments Commenced May 29, 6:30 A. M., Terminated May 31, 7:00 P. M.

♀ No.	Age Days	Date and Temperature						Number of Responses	Remarks
		5–29 64–68 °F		5–30 60–68 °F		5–31 °F			
		A. M.	P. M.	A. M.	P. M.	A. M.	P. M.		
582	1	.....	9½, 11.....	4½, 8, 11.....	.....	.....	7.....	6	
559	1	7.....	.....	11½.....	1, 9.....	7.....	.....	5	
560	1	.....	.....	.....	.....	.....	.....	None	
574	1	.....	.....	.....	.....	.....	.....	None	
587	1	.....	.....	.....	.....	.....	.....	None	12 normal females made 29 flights or .2 5/12 flights per ♀ with a temperature of 64–68 °F.
500	3	.....	.....	.....	.....	.....	.....	None	
501	3	.....	6½.....	.....	.....	Died.....	.....	1	
506	3	.....	9½.....	.....	1½, 2, 9.....	.....	.....	4	
508	3	7.....	8.....	.....	.....	.....	.....	2	
510	3	8.....	7½.....	.....	9.....	.....	.....	3	
499	3	.....	.....	.....	.....	.....	.....	None	
455	6	7, 8, 9, 10, 11, 11½.....	2, 7½.....	.....	.....	.....	.....	8	
Total	.....	.....	.....	.....	.....	.....	.....	29	

EXPERIMENT D

TABLE 10

NORMAL CECROPIA, FEMALE

Experiments Commenced June 3, 9:30 P. M., Terminated June 6, 7:00 A. M.

♀ No.	Age Days	6–3 68–70 °F	6–4 70–80 °F		6–5 70–80 °F		6–6 70–80 °F		Number of Responses	Remarks
		P. M.	A. M.	P. M.**	A. M.	P. M.*	A. M.	P. M.		
26	½					6¾, 7		Experiments terminated	2	
28	½					7½, 9			2	
29	½					7½			1	
20	½	9¾	9						2	
24	½		3½			7½			2	
32	1		3½, 8½, 9	8			2¾, 7		6	14 ♀'s made 63 flights or 4½ flights per ♀ with temperature 68–80 °F.
33	1	10¾	3½			7½			3	
34	1		3½, 8½, 9	8	10	6¾, 7½, 11	2¾		9	
35	1	10½	3½, 8½	5½, 8		6¾, 7½	7		8	
39	2		3½	8		6¾, 7½, 11¾			5	
41	2		3½	3, 8		7½	7		5	
47	2		3½, 8½	3, 5½		6¾, 7½	2¾		7	
50	2		3½		11½		7		3	
44	4	9¼	3½, 8½, 9	1, 5½		7½	7		8	
Total									63	

*No experiments were made or observations recorded on June 5, between 11:30 A. M. and 6:45 P. M.

**The moths that responded were replaced on wall and no experiments were made or observations recorded before 10:00 A. M. next morning. It is strikingly strange that during this period 8:00 P. M. to 10:00 A. M. next day only one female responded.

each, as compared with 2½ flights each for those of the first lot when the weather was ten degrees cooler. This indicates a marked increase in activity during the warmer days, but since the males which were under experimentation at the same time showed a slight decrease in activity at that time, the difference is probably due to something other than temperature.

These, like the males, showed no tendency to move simultaneously; some flew promptly and often, and others waited as long as 48 hours before making a start or repeating a flight.

An attempt was made to study the reaction to light of blind cecropias. This work was done simultaneously with Exps. A and C. The eyes of 17 males and 10 females (see Table 11) were painted with two coats of black stove enamel; this, it seemed to me, should have permanently ended their vision without causing them to suffer the shock of mutilation, but I have no guarantee that it actually did so. The males under these conditions averaged just one-half the number of flights accomplished by normal males, in the same place and time; out of the 17, Table F, only 4 failed to respond. This shows at least that some were materially affected by the change, although the surprising thing is that any of them found the light. Of the females, only 4 out of 10 found their way to the light. This amount of efficiency may indicate the presence of some unknown sense whose very existence we have not suspected, but I am more inclined to attribute it to faulty technique, such as cracks forming in the painted area. I should like very much to see these experiments repeated, if some method could be devised which would be more efficient than painting the eyes without causing a severe shock to the moths. If the rhythmic periodicity of these creatures is a thing inherently fixed within their beings as a physiological process instead of a psychological one, then we should see those deprived of light stimulus reacting at certain periods of the day. Even after making generous allowance for faulty technique, I see no indication of this concerted reaction.

The same work was carried on simultaneously with polyphemus males and females. They displayed much greater variation in the number of trips to the light than did the cecropias. Among the males, some waited long and seemed satisfied with one trip; others kept coming to the light as fast as I could carry

TABLE No. 11

EXPERIMENT E — BLIND FEMALE CECROPIAS

Time, Temperature, Technique Same as Table 9

Female No.	Age	5–29 A. M	5–29 P. M.	5–30 A. M.	5–30 P. M.	5–31 A. M.	5–31 P. M.	Number of Responses	
592	½							None	
591	½							None	
579	½							None	
577	½							None	
580	½			6½				1	
540	1							None	
498	3							None	
482	3		6½		9			2	
481	3			4½				1	
477	3							None	10 blind ♀'s made 4 trips, an average of 4/10 trip per ♀.
Total								4	

EXPERIMENT F — BLIND MALE CECROPIAS

Experiment Set on 5/28 at 11:15 P. M., First Observations Next Morning at 7:00 A. M.
Temperature, Technique Same as Table 9

596	½							None	
595	½			4½				1	
594	½			4½, 11½	1	7	7	5	
544	1	11½					2	2	
543	1	7			9			2	
542	1						2	1	
541	1	10		4½				2	
532	1	7, 11½	11		9	7		5	
531	1	7, 8	5½	4½		7		5	
530	1	8	6½, 7½	4½	9	7		6	
529	1	8, 9			9	7	2, 7	6	
484	3							None	
483	3	8	5½, 6½, 7½	11½	2, 9	7		8	
480	3	7	5½	4½			2	4	
479	3	7	7½	4½		7	7	5	
470	3							None	
462	6							None	17 blind ♂'s made 52 trips, an average of 3 1/17 trips per ♂.
Total								52	

them back, and would have come oftener if I could have kept up with their speed. The number of trips made by the 17 males were as follows:

Trips.	No. of Males.
1 to 9	7
10 to 19	6
20 to 29	1
30 to 39	1
40 to 42	2

The high or low number of reactions did not occur on any one day, so one cannot say that conditions of environment caused them.

The polyphemus females showed surprising promptness in flying to the light, but the experiment was set at 9 p. m., the hour at which the moths become busy. In fact, 7 of the 12 females had responded within the first 45 minutes, in spite of the fact that the only light was that which came in at the third floor window from the street lights below. They did not continue their activity, however; one of them remained absolutely indifferent during the three days of experimentation, 9 responded only once or twice, and the other three made 7, 10 and 13 flights respectively. The very fact that some females should respond so many times would lead one to suspect that learning or the innate possibilities to reaction is much more pronounced in some than in others. These simple experiments reveal that there is abundant variation in their reactions to light stimuli. Phototropism, at least, does not victimize the entire population at the same time and in the same way.

The Light of Dawn.

The time of flight of the majority of wild cecropias was the hour of dawn, about 3:30 to 4:30. This hour was divided into thirds, and records kept for eight days of the number of moths that came in during the darkest 20 minutes, the medium and the lightest 20 minutes, which was the full morning light just before sunrise.

May.	3:30 to 3:50	3:50 to 4:10	4:10 to 4:30	Total
21	25	31	37	93
22	58	30	11	99
23	5	2	1	8
24	33	28	12	73
25	13	22	6	41
27	16	41	12	69
28	.....	21	12	33
29	16	6	6	28
.....	166	181	97	444

Thus, of these 444 males, 38 per cent came in during the 20 minutes when the light was scarcely distinguishable from night, and 40 per cent during the medium light, leaving only 22 per cent of the moths abroad as the full light of day approached. We are safe in assuming that the majority of those which arrived after daybreak had probably aroused themselves and started on their journey during the darker portions of the hour. Some further records were kept to see if this distribution over the period covered the various classes, the wild old males, the wild young males and the bred males, but no evidence was found to indicate that one period influenced one class more than another; all three periods contained members of all three groups.

I have frequently referred to the cecropias coming in at dawn. This would imply that the moths become active with the first streaks of light, which was not true, for at 3:30 a. m. the blackest night prevails, that proverbial blackness which precedes the dawn. This brings up the question, "When does dawn begin and when does it end?" At first this seems a foolish question, but since these creatures are very sensitive to light, and it is a factor of so great importance in their existence, this is an important question. It is difficult indeed to believe that light alone at 3:30 a. m., can be the stimulus to their action, when it seems to the human eye in no wise different from the light of other night hours.

A critic of course might say, that this is the hour of their activity, and come what may, when that period recurs they must and will fly, and they can not evade it. If he made that statement about cynthias, he would be more nearly right, but it is not true for cecropias, for their movements are actuated not by

the hands of the clock, but by optimum conditions of light. This has been adequately proven in the experiments.

In order carefully to study the light conditions of this period I set the alarm at 3:25*, and was on the roof at 3:30, waiting for the first moth to arrive. At that time there was in my estimation, absolute darkness, broken only by the stars and artificial lights of the city. My brief notes were made only by means of a flashlight, which I could turn on for only an instant. Not until 4:08 did it become sufficiently light that I could clumsily guide my pencil on the paper without the aid of the flashlight. By the time their flight ceased, about 4:30, the gray light of day awaited the sunrise. Hence, to my senses, dawn was at about 4 a. m. Of course it is easy to understand that if the conditions at 3:30 aroused the moths to flight, those which were near would come in at once, while those which came from great distances would arrive later, unless the dazzling light of sunrise overtook them en route and stupified or lulled them into quiet for the day. This sounds logical, yet in my attempts at imitating in the laboratory this condition of intense darkness, I could get no reaction, but when I produced a condition of light similar to that at 4 o'clock, there was some response. Of course the artificial lights of the city modified the darkness, but they had been there all night, as had also the females in the cages, which were emanating their odors from my windows all through the night when no males came in. Hence it seems that in nature there is an optimum condition of diffused light to which alone the cecropias react. Some supersensitive males can perceive the coming of the dawn before it is evident to others; some are so dull that the light of day is not perceived until it is well upon them, and come in at the last end of the procession, in very human fashion. Then there is the great class of respectable citizens who do the right thing at the right time, and come in midway in the period. Then there is the exceptional individual who reacts to the light he sees or thinks he sees long before his fellows. Lastly there are those of dull sensibilities who never arrive at the goal; how great this horde is I shall never know. So while the moths as a class respond to a certain intensity of light, their response is modified by individual temperament.

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*On many nights, as the data show, I was up on the roof all night, and I know that (with the exceptions recorded) none came in before that time.

FINAL SUMMARY.

A few outstanding facts may be gleaned from the foregoing pages, as follows:

1. The sex life of the various species of Saturniid moths is very definitely interlocked with rhythmic periodicity, and that rhythmic periodicity is affected by conditions of light.

2. During the period of their flight, recurring once in each cycle of twenty-four hours, the males fly to the females from different distances, varying from a few yards to a maximum distance of three miles. (No greater flights were attempted.)

3. The various distractions encountered en route, city street and automobile lights, house-tops, street odors, city smoke and beating rains offer no hindrance to males responding to the attraction of the females.

4. The work shows that the number of marked males that fly to the females is in inverse ratio to the distance from the point of liberation.

5. Evidence throughout the experiments proves that the males reach the females by odor perception, and that wind is the agent by which the odor is carried. When the males are liberated elsewhere than in a current of air blowing direct from the females, few or none find the female.

6. The general term "night fliers" should not be applied to these moths, for each species has its own brief period of flight during the cycle of twenty-four hours. The moonlight sometimes influences the period of flight in some species.

7. While odor is the influencing medium inducing the nuptial flight, the attraction cannot be termed chemotropism, since trial and error method play an enormous part in locating and finding the female.

8. The male is an ardent lover, and while the females are often inactive, not all are mere bundles of inactive, odoriferous matter, but some females strongly display sex emotions.

9. Each species regularly has its short period of activity. This rhythmic periodicity can be changed to a considerable degree in Cecropia by simulating dawn conditions at high noon. In Cynthia, the hour of activity is more deeply set and cannot be changed so readily; therefore we think Cynthia is phylogenetically the older of the two species. The fact that the various

species of Saturniids in one locality have different periods of flight helps, of course, to keep the species from interbreeding.

10. The seat of odor perception is probably located in the antennae. Complete removal of these appendages renders the male incapable of finding the female. The part of the antenna containing this sense organ is undoubtedly the basal region, since removal of only a portion of each antenna does not impede the action of the male, and neither does blinding the eyes of the males adversely affect it.

11. Light rays of certain intensities exert greater influence in first arousing the males of all four species than do females, for they will often ignore a nearby female to fly to a stream of light coming in at a distant window. While the heavily ova-laden females are supposed to be more or less sessile, they too attempt, in a goodly portion of cases, to struggle (they are too heavy to fly) to the light.

Throughout these pages the reader is often reminded of the crudity of the technique, of the improvised apparatus, and the limitations encountered in turning one's home into a Saturniid laboratory. By this time the thought doubtless enters the mind of the reader that experimental work on light reactions, odor responses and wind velocity should have the benefit of a well appointed laboratory. The writer had not gotten far into the experiments before he keenly felt the need of such apparatus. But making the most of any material at hand, he succeeded without refined machinery in clearing up several puzzling problems in the lives of these mysterious creatures.

However, the last word has not been said on sex attraction and rhythmic periodicity in these moths. Some of the problems can be solved with crude, improvised apparatus, and others require the use of the highly technical apparatus of a psychological laboratory. From time to time during the course of the work, I jotted down these unsolved problems, and I record them here in the hope that some one with adequate facilities will undertake their solution.

Long distant experiments, five- or ten-mile flights, with a careful study of wind direction and velocity, and a study of the relation of wind velocity to speed of flight.

Horizontal flight vs. vertical flight. In these tests all the work was done on a horizontal plane. In a vertical test flight

the females could be placed on the roof of a very high office building and the males liberated on the street immediately below.

Rhythmic periodicity in relation to sleep, hypnosis, catalepsy, lethargy and wakefulness.

Differences of odors given off by the sexes of each species.

Homing flights in brisk, cool winds of early spring, and in the warm breezes of summer.

The function of the eyes. Their eyes shine with cat-like brilliancy at night, but since they need not eyes for either food or mating, what can be their use besides perception of light?

If the rhythmic periodicity in certain species is fixed and cannot be changed by experimentation, does this set rhythm vary in different strains of the same species (i. e., material from different localities)?

Effect of temperature on the action of the odor glands, i. e., does an increase of the temperature of the wind passing over a female increase the emanations?

Experiments in progressive liberation; liberate various lots of moths in a favorable wind, at intervals of an hour, and at various distances, and then time the returns. A concrete example would be to liberate many male prometheas at 2:30, 3:30, 4:30, and 5:30 p. m., at distances of 2, 1½, 1 and ½ mile respectively.

Experiments in response to moving lights in contrast to stationary lights.

Rule out light completely, and see if odor plus wind excite response.

Reaction of males to odor of females of other species.

DISCUSSION OF SENSES

The five senses possessed by Man may also reasonably be attributed to most of the insects. In the Saturniids, however, the sense of taste is eliminated, since they take no food. This leaves only four senses of which we have positive knowledge: hearing, seeing, touching and smelling, for the guidance of the males of these moths when they fare forth in their quest of mates. We have seen that the males travel distances up to three miles to reach the females. They set out when light conditions reach the intensity at which their species is aroused to activity. I have no reason to believe other than that this light perception is re-

ceived by the eyes. The light condition perceived by the eyes influences the moth to the activity of promiscuous flight by which he comes sooner or later into the odor stream of the females. This odor is perceived by the organs of olfaction probably situated in the antennae. Under natural conditions the sense of touch might assist in finally bringing the sexes together, but this is only secondary, since I have seen males trying to mate with females inside a wire cage where contact was impossible. Sometimes the vibration of the female's wings against the cage produces a musical sound, but in the open I doubt if they produce more than a vague rustling. No other evidence has at any time been observed which would indicate the functioning of auditory powers in the meeting of the sexes; nothing has indicated the presence of sounds outside the range of the ear of Man. This, then, reduces the number of senses involved in the coming together to two, seeing and smelling. We must not forget that without a condition of light to arouse the males to flight, and without wind to carry the odor which they follow in flight, there is no mating.

Mayer thinks that the attraction of the male to the female promothea is due to chemotaxis. If following an odor trail to its source by hit or miss methods is chemotaxis, then the term may stand. If I walk along the street and catch a whiff of boiling sauer kraut, and poke my head into several restaurants until I find the one which stews the kraut, my action could hardly be called chemotaxis. If, however, you only saw me sniff and enter the last restaurant without having seen me explore the others, you would interpret the behavior as chemotaxis. Mayer comes upon the scene and, finding males about his cages, he immediately says "chemotaxis"; had he singled out numbered or individual males, and with note-book in hand recorded their gyrations to and fro, up and down, in and around, leaving and returning, he would dispense with this term and simply describe the action as trial and error in response to odor.

While Mayer and Soule say that the phenomenon which they witnessed in *C. promethea* and *P. dispar*, is chemotaxis, they surely do not mean to use the term in the sense of Loeb. They really mean finding the female by sense of smell, for they say: "frequently we have observed a male flying up against the wind until he passed by the side of and beyond the female,

where he would often remain poised on the wings and the wind would drift him back until he came leeward to the female, when a few vigorous strokes of his wings would bring him more or less toward her again." . . . "In other words, speaking of the male being attracted and ferreting out the female in these two species of moths, the male pursued the method of trial and error so ably shown by Jennings to be prevalent in the animal kingdom."

Turner has shown that Saturniid moths, polyphemus and cecropia, perceive sounds, and moreover have been taught to associate certain sounds with pain. It seems to me that hearing in these creatures is for the purpose of avoiding enemies, and not to locate mates. I cannot agree with Mr. Frank E. Lutz* when he says: "In the case of some moths, the males are supposed to locate the females by odor. . . . Incidentally, it may be said that none of the experiments believed to have demonstrated that odor is the guiding factor in the case of moths, have absolutely ruled out sound, and male moths have antennae quite as plumose, apparently, as well fitted to receive sounds, as those of male mosquitoes."

I think my simple experiments where males were in close proximity to females in the same cages, and mating did not occur, because there was no wind to carry the female odor, demonstrated the error of this view. It might be possible for the female moth to emit sounds that transcend the human ear, but surely it would influence the male if such sounds were emitted by the female when he was only an inch or two away. Likewise in the glass box experiments, where the females could have emitted sounds and probably would have done so at this time if they ever do so, to attract the males, we see perfect indifference so long as the air is motionless. Again it seems logical to assume that a five- or six-day old female would be more proficient in the art of communication than one a few hours old if her attractiveness depended upon audible expression. It is well known that fresh, young ones wield the greater sex attraction. Of course Mr. Lutz will admit that something other than sound excites the males to copulation when he remembers the work of Freiling[1] and of Kellog[2] on the silkworm moths, *Bombyx*

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*Bull. Am. Mus. Nat. Hist. 50:337. 1924
[1]Quoted by McIndoo, loc. cit. p. 55.
[2]Biol. Bull. 12: 152-154. 1907.

mori. The former made a careful study of the scent producing organ of this moth, and considers it the most highly developed scent producing organ in the Lepidoptera. With pieces of filter paper he succeeded in drawing from these sacs some of the secretion, and then placed the paper in front of freshly emerged males. The males at once threw themselves upon it and behaved as if the paper were a female. Kellogg obtained similar results, and says: "If the cut out scent glands are put by the side of but a little apart from the female from which they were taken, the male always neglects the nearby live female and goes directly to the scent glands" and tries to copulate with them.

Of the butterfly, *Pieris protodice*, Rau[3] says of a pair that were trying to remate after having separated, "The female dropped several inches to a lower stratum of leaves and remained for a few seconds, and then darted away. I expected the male to go in hot pursuit; instead, for the next ten minutes while the female was dancing over some shrubs a hundred yards away, this male was frantically going in and out among the leaves in the spot where the female had paused." His frantic search was pathetic to see, while a short distance away the female was dancing in full view. If the attraction were sight or hearing, he could easily have followed her, but the only thing that held him was the odor left by the female in the bushes.

Fabre, in Chapter XI of "The Life of the Caterpillar" is much impressed with the behavior of the males of several species of moths nearly akin to the material experimented upon in this paper. In order to give the foundation for some of his conclusions we here give details from his experiments.

A captive female of the "Great Peacock" moth brought hordes of males "coming from every direction." He removed the antennae of six males that came in, let them fly out at leisure, and then apologizes because only one returned. In the light of the experiments of Kellogg, Mayer, myself and others, it is surprising that even one returned. I suspect that the one never got far from the room, and the find was accidental. In a second experiment in a similar situation, involving 16 antennaless males, none returned. In a third test, 14 marked males with full antennae were permitted to escape from the

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[3]Journ. Anim. Behav. 6, 367, 1916.

room; of these, only two returned later. This fact worried Fabre greatly, and he tried to account for the non return of the twelve by the surmise that the "Great Peacock is worn out by the ardours of pairing time." He forgot for the moment that the two that did return were under the same strees of pairing time. Fabre says that they lived only two or three days and in the same breath says that the female lived eight days. It seems probable, therefore, that their failure to return was due to other influences than short life.

Perhaps Fabre's reluctance in accepting odor and wind as the factors which bring them together is due to his impression that they came from all directions. Without careful outdoor observations, how could he tell but that the behavior was the same as Mayer and Soule found for promethea flying against the wind as mentioned above.

Fabre, however, at one period in his peacock work, really suspected odor as the agent, but when males were still attracted to females even when he placed napthaline in the room, his "confidence in the olfactory explanation is shaken." He for the time forgot that the napthaline odor meant nothing pro or con in the life of this moth; it was something entirely outside its experience in the natural world. But really Fabre must have thought better of the "olfactory explanation" than he was willing to admit, because next year when he got poor results he says: "low temperature is unfavorable to the tell-tale effluvia, which might be enhanced by warmth and decreased by cold, as happens with scents."

The third year he got large numbers to fly to the females; he moved the latter about each morning and then says: "all of these sudden displacements contrived to put seekers off their scent do not trouble the moths in the least." Even then he was not ready to give odor and odor perception any credit, for he suspected "wireless telegraphy by means of Hertzian waves is the means for attracting the males." He soon rejected the idea of wireless telegraphy as a means for attracting the males, when he lodged females in air-tight boxes of various materials and got no males to respond, but he did get them to come when he placed the females in poorly closed and cracked receptacles. In his work on the Lesser Peacock moth, *Attacus pavonia minor*, he says they arrived "with a tortuous flight." The flight, it

seems to me, would not need to be tortuous if the moths were flying with the wind, responding to a wireless telegraphic message.

His next species for study was the oak-eggar or banded monk moth. A female brought males "hurrying from all directions," about sixty keeping up their frenzied movements for three hours. He found that in this species also the males would find the females hidden in various kinds of receptacles, provided they were not too tightly closed, but they also did not find them in vessels hermetically sealed. Fabre then placed stenches of various kinds near the female in such abundance that he nearly asphyxiated her, thinking thereby to make her unrecognizable to the males. Numerous males arrived just the same, and made desperate efforts to reach her. Fabre then placed the female in a bell-jar on the window ledge, in full view of the incoming males, and threw the old wire cage upon which she had rested into a far dark corner of the room. The incoming males completely ignored the female in full sight and flew to the far corner of the room, and spent all the afternoon dancing around the deserted home which had held the prisoner some hours before. Of course since it seems improbable that the old wire dome threw out Hertzian waves to which the males responded, Fabre concludes that "it is smell therefore that guides the moths, that gives them information at a distance." Fabre then playfully placed his females for various periods on glass, wood, marble and cloth, and watched the males come to the objects, attracted there by the odor left by the female. He gives wind credit for naught, says nothing about it except of its impotence in the behavior of the moths. He does not face the final question of why the males came to that very room in that very house, if it were not that some of the odor-laden air passed out of the house and mingled with the passing winds. He concludes: "But what we are to say of the great peacock and the banded monk making their way to the female born in captivity? They hasten from the ends of the horizon. What do they perceive at that distance? Is it really an odor as our physiology understands the word? I cannot bring myself to believe it. * * For all his finess of scent the dog is incapable of such a feat, which is performed by the moth, who is put off neither by distance, nor the lack of any traces out-of-doors of the female hatched on my

table.'' Unfortunately, he has no actual knowledge of whence they came or how far. Because he suspects that they travel very great distances, so great in fact that he cannot conceive that odors can travel so far, he tries to account for the behavior in new and mysterious ways, for he says: ''Like light, odor has its X-rays. Should science one day, instructed by the insect, endow us with a radiograph of smells, this artificial nose will open out to us a world of marvels.''

No new device now seems needed to open up a new world of marvels in this instance. My investigations show clearly that there is a limit to the distance males can travel to reach the females. The further away from the females they are liberated, the fewer will return. Fewer will return from three miles than from a half-mile, and those which do make the long distance are exceptional individuals. Without wind bearing the female odor there would be no attraction of the males. It is easy for me to believe this, since I have myself repeatedly caught whiffs of cecropia odor on the breeze, although my olfactory organs are not especially attuned to these emanations. O. W. Richards* in speaking of Mayer's work on *Callosamia promethea*, makes this very pertinent remark: ''The distance that males are attracted is probably often exaggerated and, in this connection it must be remembered that the males of these forms have often a very erratic flight, coursing about in all directions.'' I judge, from observations in the laboratory, that they are inactive until the time for flight, and then fly at random until they find an odor trail.

Fabre and others constantly remind us that there is no similarity between our sense of olfaction and that of the insects, but Bellonci† finds, in studying in a comparative way the olfactory lobe of the lower vertebrates and the antennary lobe of insects, that the histological structures of these organs in the arthropoda have a very close relation to that of the olfactory lobe of vertebrates, and concludes therefrom a physiological if not a morphological homology. Forel is willing to admit ''that the olfactory bulb and the nasal mucuous membrane of the vertebrates are derived from the invagination of the antenna and the antennary ganglion of an invertebrate. The nerve terminations,

*Biol. Reviews 2:320. 1927.
†Cited by Forel, Senses of Insects, p. 96.

formerly protruding, are sunk in a cavity which is placed in communication with the pulmonary organ of respiration, which allows of a current of air continually renewed to bring odors to them." "For my part, I believe that this homology is true. Then the antennary ganglion will become the olfactory bulb, its nerve terminations will be the numerous little olfactory nerves, the antennary nerve will become the *tractus olfactorius* and the antennary cerebral lobe will become the olfactory lobe."

"But the antennae of insects are an olfactory organ turned inside out, prominent in space and certainly very mobile. This certainly allows us to suppose that the sense of smell may be much more relational than ours, that the sensations thence derived give them ideas of space and direction which may be qualitively different from ours." "In reality a sense of smell which admits of distinguishing space is a kind of sixth sense very difficult for us to describe. But all evidence points to the fact that insects with mobile antennae have such a sense. In this way the sense of smell directs them much better than mere perception of odors. This fact also explains how ants distinguish the right side from the left side, the front from the back, by their sense of smell, and know when following a track or a trace, in what direction they are following it. Finally, pursuant to the laws of association, it allows insects an olfactive memory of places such as relational sense alone posesses."

It is gratifying indeed to find that comparative anatomy thus gives us morphological substantiation for our findings in the field. Forel says, "A sense of smell which admits of distinguishing space is a kind of sixth sense very difficult for us to describe." It may be difficult in the case of the tiny creatures, ants, with which he worked, but a little careful imagining on a larger scale and comparing with other sense organs will make it clear.

Among our own five senses, only three—sight, hearing and possibly smell—bring us information on distance and direction of distant objects; touch and taste have no part in this. Let us consider the simple mechanics of these three organs in ourselves. We receive visual impressions of an object by the turning of the eye, the adjustment of the muscles, in that direction; we can estimate distances only by the muscular converging of

the two eyes. This is a marvelous feat. We can tell the direction whence comes a sound only by turning the head to and fro and focusing, as it were, the two ears on the sound. This seems unbelievable, yet we do it every day. In like manner we turn our heads this way and that in an attempt to determine from which direction the odor is strongest, or we feel the breeze, the vehicle of odor. The olfactory apparatus with which we are now equipped functions very poorly in helping to determine the direction of an object emitting an odor. Our receiving organ is merely a single immovable area of mucous membrane, within the head, where the air drawn in by respiration may touch it. Now let us imagine ourselves equipped with such olfactory organs as he ingeniously describes for these moths, "a branching olfactory system turned inside out." This would be a pair of external olfactory organs, much branched, symmetrically placed on the body as are our eyes and ears, mobile as are our eyes, and lastly, extending out in front of us one-fifth the length of our bodies. It is easy now to understand how such an apparatus could serve the organism better than either visual or auditory powers (as we know them) in guiding it to the source of the emanations. There is reason to believe that wonders would be accomplished by means of such a mechanism which would far exceed the marvels of sight and hearing. But, we must not forget, while this apparatus would be more powerful or efficient in detecting directions, its scope would be limited to a narrower field, because, unlike light rays or sound waves, which radiate in circles, odors are carried on the wind in a stream in only one direction. The greatest distance at which Man's degenerate olfactory sense will function is not known to me, but I once heard a man, whose scientific accuracy could be relied upon, say that in the wilds of Montana, where only wood was used for fuel, he had often smelled coal smoke from a train from a distance of fourteen miles, in the clear air.

Thus the "magic" and "mysterious sixth sense" which have been adduced to account for the attraction of these moths to their mates may readily be brought within our comprehension. I still maintain, however, that the creatures do not come "from the ends of the earth," but that their flight in this quest is limited by the area of dissemination of odor in currents of air.

DISCUSSION OF RHYTHMIC PERIODICITY.

Bouvier, in his already mentioned chapter on "Rhythms," in agreeing with Loeb, says that in certain moths "This periodicity is independent of actual luminous stimulations." To some extent the experiments of Reaumur, whom he quotes, influences this decision. Reaumur says of moths enclosed in boxes and cages that during the day they are quiet in their prison, "passing hours and often days without moving in the same place. But when night has come and even before the sun is set, they move their wings and fly as much as the box will permit." Of course this quotation seems contradictory inasmuch as they cannot spend days in their prison without moving and at the same time become active when night comes. What probably happened with these moths was that some were placed in light-tight boxes, and these spent days without moving, while those which were in cages, where natural light could penetrate, responded to the dim rays of optimum intensity. By referring to our experiments, one can readily see that this is what happened in cynthia, cecropia and polyphemus. In tests in light-tight containers, they did not move from their marked places for several days at a time, but became active only when dim light was admitted. Obviously the statement that "periodicity is independent of actual luminous stimulations" does not hold for the above three species. Despite the fact that Reaumur's statement, quoted above, gives us no assurance that his "boxes and cages" were light-proof, and hence there is nothing to show that the moths react in absolute darkness, Bouvier goes on to say that "this is a periodicity acquired by the organism. This is graven upon the being in the course of generations under the phototropic influence of periodical luminous stimulations and may show itself today without their intervention. It has separated itself from the stimulating actions which have produced it."

Also from Loeb's observations on the sphinx moth carried on "during two or three days," Bouvier concludes: "Thus the periodicity appears to us to be manifest and independent of luminous variations." But unfortunately, in the next paragraph, also based on the experiments of Reaumur and Loeb, he concludes: "Thus understood, the periodicity shows itself to be a simple manifestation of phototropism with these insects."

Concerning Roubaud's observations on the larvae of the African fly which come out of the earthen floor at night to feed upon the natives sleeping on the bare ground, he concludes: "This periodicity is the result of thermic sensibility. This rhythm not only is acquired in the course of the larval existence, but is changeable at the will of the experimenter." These and other conclusions drawn for the most part from inadequate observations, are obviously self-contradictory.

But this condition of chaos in the literature regarding rhythmic periodicity serves to bring to light a significant point in this new field of study. It is evident that this comparatively new term, rhythmic periodicity, has caught the ear of many investigators, and intrigued them to either attempt to explain the phenomenon without defining it, or more often, to apply the fascinating term, as though it were a final explanation, to any regularly recurring action discovered in their material. Thus in the above instance, the action of the African fly larvae in coming out at night to feed upon the natives when they lie down on the ground is ponderously explained; "This periodicity is the result of thermic sensibility," although a few lines further on the author naively explains that the creature's "rhythm is changeable at the will of the experimenter." To call this action "rhythmic periodicity," when the creature merely turns to its food supply when the latter intermittently comes near, is obviously far-fetched. Many phenomena explained by various authors as "rhythmic periodicity" are merely adaptations or even temporary adjustments to a regularly recurring feature of the environment. The clover spreads its leaves to the sun during the day to make its growth; the rabbit slips out to nibble the clover at night so he may escape the hawk; the owl sleeps during the day so he may come out and get the rabbit. All of these actions, taken separately, have been attributed to rhythmic periodicity, yet not one of them would continue its action rhythmically (by the clock) at all if the object of its quest changed habit. Of course these adjustments to environment or fellow-creatures entail morphological modifications in the organism—the eyes of the owl, the eyes of the hawk, etc., but whether the habits have caused structural variations, or whether morphological changes have induced new habits is a problem that is outside the scope of this paper. Pursuing a

little further the example given above, the night and day temperature of the owl has already been cited as an example of the action of rhythmic priodicity. Most birds are slightly warmer during the day than at night, but the owl's temperature rises during its nocturnal time of activity. In most cases the observer neither asks nor answers the question of which is the causal and which the resultant character; but, fortunately, in this case Elton makes his data significant by telling us that the temperature variation of the owl may be reversed by reversing its periods of activity and rest.

Our search for authoritative rhythms, *rhythms which dictate terms to the organism,* continues. The sleep of birds seems rhythmic; a rooster makes an excellent alarm-clock, provided you are willing to be called at four in the summer and six in the winter and allow him an extra crow after a midday eclipse. Probably one of the most persistent rhythms we can cite is that of the menstrual interval in mammals, yet climate, environment, disease and even occupation break the measure of that rhythm.

But despite the fact that our experiments on these three moths show that light of a certain quality is the controlling factor for activity, and the habitual or rhythmic program of these creatures may be caused to vary by manipulation of the light, yet we must acknowledge the presence of some undiscovered controlling factor, or else something ingrained in the organism that makes them respond in the open at the period when they do. The unanswered question which still baffles us is this: If light rays of a certain intensity were the sole cause, why do the moths not flock to the females when the sun is at an equal distance below the horizon in the west (evening) instead of the east (dawn)? It may be that the physicist will be able to tell us that the light of dawn comprises rays which are different in kind from the rays of numerous artificial lights of the city. It is quite possible that the visual organs of these creatures are adapted to receive the violet rays or something akin, which our eyes do not perceive, and which are not present in the artificial lights, but I can hardly imagine that the physicist can tell us of differences in the rays of light shooting out from the sun an hour below the horizon in the west and an hour before appearing in the east. We may, with equal fitness, apply this same question to the activities of the day-flying prometheas, which fly only in the late afternoon.

Thus the powers and limits of rhythmic periodicity are exceedingly difficult to define. That such a condition exists, that these actions occur regularly in nature, we shall not for a moment deny. Yet we find that most of these rhythms are modified by changes in related conditions, either within or without the organism. Of course, we ultimately arrive at the realization that the rhythmic periodicity of any organism is only that creature's share in the "Harmony of the Universe"; so long as the planets swing in rhythm, with regular seasonal and day-and-night changes on our earth, all living matter must of necessity move in harmony with these (or other resulting) cycles. Hence many kinds of behavior are explained as rhythms, which are only adaptations to the rhythm of the whole. Only a small beginning has been made thus far in the study of this fascinating subject. It can probably never be singled out alone, for it is inextricably intertwined with adaptation, habit, sleep, fatigue, stimulations, psychogenesis, etc.

The results of the present study regarding rhythmic periodicity are two-fold. First, our findings agree with Davenport's interpretation of earlier experiments when he says that nocturnal moths are so constructed that they react only to feeble luminous intensity, whereas diurnal lepidoptera react to rays of high intensity. The second is that rhythmic periodicity within the organism can rarely be regarded as a causal factor or phenomenon, but only as relational, showing the interdependence of creatures or a creature and its environment. It is usually no more than a creature's habitual adjustment to its surroundings, but there are no doubt many instances wherein rhythmic action is truly an innate character of the tissue, as the pulsations of the heart-tissue of the early chick embryo. At the present moment I am inclined to say that those actions which require a stimulus to start them are only reactions, or adaptations in behavior, while those actions which require outside interference to stop them or modify them may be truly termed rhythms.

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THE PRAIRIE HORNED LARK

Gayle B. Pickwell

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Plate I (Frontispiece). The Prairie Horned Lark Reviews Her Nestlings.

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By

GAYLE B. PICKWELL

THE PRAIRIE HORNED LARK

By Gayle B. Pickwell

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INTRODUCTION

The Bird.—Out at the bleak end of that ecological series of bird habitats, that begins with the heavy forests and ends with the barrens, lives America's only Lark, *Otocoris alpestris* (Linn.). In that region extending from the Missouri to the Atlantic and from Kansas to Ontario the particular form of this Lark is *Otocoris alpestris praticola* Hensh., the Prairie Horned Lark. Far from the treeless Arctics, far from the deserts, *Otocoris alpestris praticola* finds as his barrens the plowed fields of the Midwest, the tree-denuded, wind-swept hill tops of the Northeastern States, those peculiarly unnatural and artificial barrens, the hazards of modern-day golf courses.

If for no other reason than that here is a bird nesting where no bird has a right to nest; a bird in a niche that demands not vegetation but lack of it; a bird alone and unique in its nesting site without a competitor and far out at the end of the series—if for no other reason than this purely ecological one the Prairie Horned Lark invites close study. But if we add to this the fact that it is a Lark, a representative of our only Lark, with the song of a Lark, the ways of a Lark and many a habit and idiosyncrasy peculiarly its own, then this account has its full excuse for being, needs no apology.

The Problem.—Desultory observations of the Prairie Horned Lark were begun many years ago in eastern Nebraska where the writer was born. Recollections of winter rabbit hunting carry also associations of Larks on the wind-cleaned pastures and great fields of fall plowing. Their nests were found on the ridges of listed corn and an observation of a song still remains clear and trenchant. We were shocking wheat (hence mid-July) when a Lark was seen climbing the air for his song. We watched him against the vivid sky during his long minutes aloft; were amazed by that final headlong drop to earth.

The intense work upon the observations for this paper was begun in June, 1925, at Evanston, Ill., continued there until the fall of 1926, transferred to Cornell University in the fall of 1926, and continued at the latter place until late summer 1927. Twenty-six nests were located at Evanston, twenty-three of which were visited daily from the time of their discovery until

they ceased to be occupied. Seven occupied nests were found in Ithaca, N. Y., and their history recorded as at Evanston.

Trips were made on two hundred and twenty-three days to observe the Larks and on many of these days the breeding grounds were visited twice. These visits were distributed by months, as follows: Six in January, fourteen in February, twenty-five in March, forty-six in April, forty-four in May, fifty-two in June, twenty-one in July, one in August, two in September, three in October, five in November, four in December.

Though efforts were made to cover all activities of the Prairie Horned Lark, yet as data accumulated there accumulated also desiderata almost as large. So that, as the problem is now brought to an arbitrary close, the things yet to be learned seem more momentous by far than the few things learned—so inadequate are two years of work, no matter how intensive.

Acknowledgments.—Daily visits to an area five miles from the Campus of Northwestern University where the writer was teaching would not have been possible except for the hearty co-operation of the members and assistants of the Department of Zoology there. Sincere thanks are extended here also to Mr. P. A. Taverner of the National Museum of Canada, to Mr. H. F. Lewis and Mr. R. W. Tufts, Federal Migratory Bird Officers of Quebec and the Maritime Provinces respectively, for information relative to *O. a. alpestris* and *O. a. praticola* of various regions of eastern Canada. To Clarice Pickwell much credit is due for assistance throughout the entire period of preparation of the manuscript. Lastly the writer is greatly indebted to Dr. A. A. Allen of the Laboratory of Ornithology of Cornell University for the opportunity he gave that the work might be brought to a successful conclusion and for his advice on many phases of the problem.

HISTORY

General.—The Prairie Horned Lark was described as a separate subspecies by Henshaw (1884, p. 263). Prior to that time all accounts of eastern writers are concerned with the "Shore Lark", or "Horned Lark", which was, most likely, *Otocoris alpestris alpestris* since *praticola* did not, apparently, penetrate to the eastern states until the later part of the 19th century.

The Horned Lark was described by Linnaeus (1758) as *Alauda alpestris* based upon the *Alauda gutture flavo* of Catesby (1731), whose figure of the bird is that of the northern form and not of *praticola* as Oberholser (1902, p. 809) has shown. Wilson's *Alauda cornuta* (1808, p. 87) was also what is now known as *Otocoris alpestris alpestris* (as witness his description: "Forehead, throat, sides of neck, and line over the eye is of a delicate straw or Naples yellow . . . ."') and Audubon's account, from notes made in Labrador, was of this bird in its home.

Since, then, most early writers are concerned with a subspecies other than the Prairie Horned Lark, their accounts will be but briefly summarized here. Wilson (1834) says of the Horned Lark: "There is a singular appearance in this bird, which I have never seen taken notice of by former writers, viz., certain long black feathers, which extend by equal distances beyond each other, above the eyebrow; these are longer, more pointed, and of a different texture from the rest around them; and the bird possesses the power of erecting them, so as to appear like some of the owl tribe. Having kept one of these birds alive for some time, I was much amused at this odd appearance, and think it might furnish a very suitable specific appellation, viz., *Alauda Cornuta,* or Horned Lark." Further he says: "I have never heard of their nest being found within the territory of the United States."

Audubon (1834) knew more than just the littoral bird of the Atlantic Seaboard for he journeyed to Labrador and found the Lark at home. His vivid description was the basis for all subsequent accounts of the Horned Lark for fifty years and little was added between the time of his writing and 1875. He says, in part: "The face of the country [Labrador] appears

as if formed of one undulating expanse of dark granite, covered with mosses and lichens, varying in size and color, some green, others as white as snow, and others again of every tint, and disposed in large patches or tufts. It is on the latter that the lark places her nest, which is disposed with so much care, while the moss so resembles the bird in hue, that unless you almost tread upon her as she sits, she seems to feel secure, and remains unmoved. Should you, however, approach so near, she flutters away, feigning lameness so cunningly, that none but one accustomed to the sight can refrain from pursuing her. The male immediately joins her in mimic wretchedness, uttering a note so soft and plaintive, that it requires a strong stimulus to force the naturalist to rob the poor birds of their treasure.

"The nest around is imbedded in the moss to its edges, which is composed of fine grasses, circularly disposed, and forming a bed about two inches thick, with a lining of grous' feathers, and those of other birds. In the beginning of July the eggs are deposited. They are four or five in number, large, greyish, and covered with numerous pale blue and brown spots. The young leave the nest before they are able to fly, and follow their parents over the moss, where they are fed for about a week. They run nimbly, emit a soft peep, and squat closely at the first appearance of danger. If pursued, they open their wings to aid them in their escape, and separating, make off with great celerity. On such occasions it is difficult to secure more than one of them, unless several persons be present, when each can pursue a bird. The parents all this time are following the enemy overhead, lamenting the danger to which their young are exposed. In several instances the old bird followed almost to our boat, alighting occasionally on a projecting crag before us, and entreating us, as it were, to restore its offspring."

Swainson and Richardson (1831) did not add to this account. Samuels (1887) and Baird, Brewer and Ridgway (1875) quote Audubon though the latter add that Nutall "started a Shore Lark from her nest on the banks of the Platte. It was in a small depression on the ground and was made of bent grass and lined with coarse bison hair", (undoubtedly *O. a. praticola* or *O. a. leucolema*). Nutall (1832) himself gives an account very similar to that of Wilson. In an earlier edition, Baird, Brewer

and Ridgway (1874) in speaking of the Horned Larks say: "starting with North America north of the United States we begin with a style absolutely indistinguishable from that of Europe, this, to which the name *cornuta* belongs, visits the Eastern States only in winter, but breeds over the prairie region of Wisconsin, Illinois and westward." These authors believed thus that *cornuta* included also what came to be *praticola*, though they remark at the peculiar breeding distribution.

The first suggestion that the Horned Lark breeding east of the Mississippi is not the same as *O. a. alpestris* of the Atlantic coast came from Allen and Brewster (1882) who suggested that it is nearer *Leucolaema* Coues than the former. Two years later Henshaw (1884) erected the subspecies *Otocoris alpestris praticola* and gave as the range the upper Mississippi Valley and region of the Great Lakes.

Extension of Range.—Partly as a result of the stimulus that followed the erection of a new subspecies in one of the most thoroughly worked ornithological regions and partly due to an actual extension of range of *O. a. praticola*, there appeared forthwith an extensive list of published notes of the occurrence of this form where previously it had not been thought to exist or had not been separated as distinct from *O. a. alpestris*.

However a few years prior to the distinction of the Prairie Horned Lark as a separate subspecies there are two or three references to a Horned Lark breeding in New York and Ontario that was, undoubtedly, this subspecies though not at the time recognized as differing from *O. a. alpestris*. The earliest of these appears to be that of McIlwraith to whom Coues (1874) refers as giving information of Larks breeding about Hamilton, Canada West (western end of Lake Ontario). The earliest publication by McIlwraith in this regard that has been located is that of his 1883 "Bird Notes from Western Canada": "Getting outside of the city we at once lost sight of *Passer domesticus*, who has not *yet* betaken himself to the farm houses, but almost immediately met with another recent addition to our birds which promises ere long to be as abundant in the country as the Sparrow is in the city. This is *Eremophila alpestris*, Shore Lark. When I first made the acquaintance of this species *twenty years ago* [italics mine], the few individuals observed came and went with the snowbirds, and kept along with them while here. They

were stout, well-developed birds, with the black and yellow markings clear and decided. Some *ten* or *twelve years* since [italics mine] a new race made its appearance, smaller in size, the colours paler and having altogether a bleached, washed-out look about them when compared with the others. These have remained permanently and increased from year to year, have now become our most common winter resident in the country. They breed very early by the roadsides and in the low commons everywhere, and at this season of the year are seen running in the road tracks or sitting in rows of fifteen to twenty along the fences waiting till you pass that they may return to their regular feeding ground''.

The above account is of great importance for several reasons. First, McIlwraith's "stout, well-developed birds, with black and yellow markings clear and decided . . . that came and went with the Snowbirds'' were, beyond question, *Otocoris alpestris alpestris* seen by him on their migrations to and from their northern breeding grounds. His ''new race'', ''smaller'', with ''colours paler'', that ''remained permanently'' was, as assuredly, what came to be *Otocoris alpestris praticola*, the Prairie Horned Lark. Secondly, critics of the supposed eastward movement of the Prairie Horned Lark (for which see further) cannot impute that these records are the results of a new interest and more careful observations which might possibly have accounted for many of the records made after publication of Henshaws' (1884) paper on the Horned Larks. Thirdly, here is an unquestioned date of the Prairie Horned Lark's first appearance in Ontario, viz., "ten to twelve years" prior to 1883, that is, 1871 to 1873. In 1894 McIlwraith, writing again of the "Birds of Ontario", says of this Horned Lark: "So far as I can remember, this species first appeared in Ontario about 1868."

The first New York record of a breeding Lark was that of the Rev. Wm. Elgin, who, as reported by Langille (1892), found a nest at Buffalo April 28, 1875. Merriam (1878, p. 53) in his "Remarks on Some of the Birds of Lewis County, Northern New York" quotes A. J. Dayan, who, in turn, quotes Dr. C. P. Kirley of Lowville as follows: ''I first observed *Eremophila alpestris* July 16, 1876, when I shot one two-thirds grown and saw the parents. In the same locality June 24, 1876, I noticed a pair of old birds, and on searching for their nest, I

found it not more than eighteen inches from the main road. It contained three unfledged young. Since then I have both seen and taken it during the breeding season." Again Merriam (1878, p. 54) in reviewing Rathbun's "Complete List of Birds of Cayuga, Seneca and Wayne Counties'' published in the Auburn Daily Advertiser, August 14, 1877, draws attention to the statement that *Eremophila alpestris* is "resident and tolerably common in winter . . . a few breed." Howey (1878, p. 40) at Canandaigua, N. Y., saw the "Shore Lark" *(Eremophila alpestris)* with a worm in the bill, May 29, 1876, "fly into a meadow". On June 11, found "an old bird with three young ones in a highway".

Merriam's (1878, pp. 54-55) comments on the above records are, in the light of later knowledge of the Prairie Horned Lark, of interest. Says he: "Mr. Dayan's note (on the authority of Dr. C. P. Kirley) is particularly interesting as it extends the known breeding range of the species *(Eremophila alpestris), within* the United States, eastward to the western border of the Adirondack wilderness, beyond which it must pass to the northward (through Saint Lawrence County) into Canada, and thence to Labrador. Whether it has for many years bred within the limits of the State of New York, or has recently extended its breeding range, as seems to be the case with the Lark Finch *(Chondestes grammaca)* and some other species, remains to be decided; I incline to the latter view. It breeds about Hamilton, Canada West (McIlwraith) and abundantly along the Labrador coast (Audubon and Coues)".

Thus Merriam, after reference to Coues' (1874, p. 38) restriction of all Horned Larks (except *Eremophila alpestris* "breeding northerly") to Iowa and Minnesota westward, concludes that the New York forms were of the northern subspecies, had extended their range from Labrador south and west! Whereas, as will be shown later, the reverse proved to be the case. Those birds "on the dry interior plains from Iowa and Minnesota westward" (Coues, 1874, p. 38) had extended their range east and north!

Further records of a breeding Lark in New York, that was undoubtedly *praticola* though published before that subspecies was erected, are as follows: Davis (1878) tells of a nest of "*Eremophila cornuta*" found at Utica, N. Y., April 15, [year?].

Lattin (1881) reports "*Eremophila alpestris*" quite common in Orleans County, N. Y., and on April 17, 1880, found a nest in an old pasture at Gaines. Later (May 28) another in a strawberry patch and June 15 *(circa)* yet another in a tobacco patch. Merriam (1881, p. 231) in his "Preliminary List of Birds Ascertained to Occur in the Adirondack Region, Northeastern New York", says of "*Eremophila alpestris*", Shore Lark: "Rare, but becoming common. Breeds on the sandy fields along the western border of the wilderness and probably at other localities." Park (1881), tells of young Horned Larks taken at Green Island, N. Y., April 22, 1881 (junction of Mohawk and Hudson). An adult pair was similarly taken April 29, 1881. Seven years later Park (1888) records the fact that Wm. Brewster identified these as *Otocoris alpestris praticola.* At the same time he mentions the taking of *O. a. praticola* at Troy, N. Y., February 22, 1883, and March and October, 1887.

Following the publication of Henshaw's (1884) paper on the Horned Larks, records of the Prairie Horned Lark are numerous and present a steady east and northward movement, followed later by a southward invasion. This can best be presented by states.

New York. Langille's, Howe's, Davis', Lattin's and Rathbun's accounts (see above) have already been given as showing the presence of the breeding *praticola* in the Adirondack region, Cayuga, Seneca, Orleans and Wayne counties and in Canandaigua, Utica and Buffalo, N. Y. (northeastern, central and western portions of the state), in 1875-1881. Park had breeding forms from Green Island and Troy (east-central border) in 1881-1887. Davison (1885, pp. 217, 218) secured the first nest and eggs of *praticola ("Eremophila alpestris")* from Niagara County (extreme western county), on June 17, 1884. The nest was in the side of a manure heap in the field. The young farmer who located it for him said it bred there three times a year for there were "young birds in April, June and August". Dutcher (1888) records *O. a. praticola* as taken on Long Island, Queen County, July 31, 1888; another, a young bird, was taken September 14, 1887.

Vermont. The earliest records of the presence of the Prairie Horned Lark in New England and of its breeding there seem to be those of Parkhill (1889). He tells of nests, presumably

of this species, in April, 1885 (three young, one egg), another in April with four eggs; a female with a nearly-formed egg was taken April 6, 1888. A positive record was made April 19, 1889, at which time the female was taken from the nest and later identified by Brewster. These records were at Cornwall. Several years later Howell (1901), records that it was first noticed in Stowe Valley, Vermont, in 1898; bred there in 1901.

Massachusetts. The first Horned Larks taken in Massachusetts that may have been *O. a. praticola* were secured by Brewster at Concord, in July, 1869. These are referred to by Howe and Allen (1901) as being recorded in Brewster's: "Minot's Land and Game Birds," second edition, 1895, p. 247. This latter reference has not been available to the writer, but it is most probable that it is this record that Coues (1874) cites from Maynard's Guide (1870, p. 121) and adds "perhaps breeding". Brewster (1888), after the erection of *O. a. praticola,* went over his collection and found a pair of Prairie Horned Larks that had been taken February 28, 1883, at Revere Beach, Massachusetts. This seems to have been the earliest definite record for the subspecies in the state. Intrigued by this February, 1888, discovery he shot twenty-three Horned Larks the next winter, December 15, 1888, at Great Island, near Hyannis, Massachusetts, and found two of *praticola* in the lot (1889). Faxon (1892) took birds in the breeding season at North Adams, and Williamstown, Massachusetts, in 1890 and 1891. Brewster, having collected the first for the state, had the pleasure of recording the first *bona-fide* nesting (1894), when Henry R. Buck reported a nest found by Buckingham with a set of fresh eggs at Pittsfield, Massachusetts, July 10, 1892. Other records of breeding followed this, the latest of significance being that of Townsend (1904), who records adults and young collected at Ipswich, Massachusetts, August 11 and 13, 1903. These and that of Forbush (1927), who shows a breeding locality on Cape Cod, place the Prairie Horned Lark at the sea.

New Hampshire. Faxon (1892), records the first breeding for this state at Franconia with records of capture of adults and second brood young of June 4 and July 21. Torrey (1905), says that it was found breeding on Mount Washington above the tree line, July 7-19, 1905.

Maine. Knight (1897), by requesting collectors to send to

him their Larks for examination, found the following to be *praticola:* Pittsfield, Somerset County, March 29, 1892, male; March 27, 1893, male; March 22, 1894, female; Bucksport, Hancock County, 1886 or 1887, two; Bangor, March 30, 1887, male; North Bridgton, Cumberland County, March 13, 1897, four; Lewiston, February 26, 1897, one. At that time the bird had not yet reached the Maine coast, nor was there evidence of its breeding within the state. Swain (1900) collected a female and young July 17, 1900, between Waterville and Pishon's Ferry on the east side of the Kennebec and so established the first breeding record for the state.

Connecticut. Woodruff (1905, p. 420) found it breeding at Litchfield, May 25, 1905, and Judd (1908, p. 129) found it breeding in Danbury.

The northward movement of the Prairie Horned Lark into northeastern Canada has been very slow and of much later date (excepting Ontario) than that into New York and southern New England. The bird must have reached these parts from New York and New England. However, because of this contiguity, the provinces will next be considered.

Ontario. It is probable, judging from its geographical position and the early date of the appearance of the Prairie Horned Lark there, that Ontario received its birds from Michigan and, secondarily, gave an ingress to New York and regions further east. McIlwraith (see above) noted that the Prairie Horned Lark first reached Hamilton (at west end of Lake Ontario) between 1871 and 1873 (or 1868 as he later avers). Fleming (1901) writes that this Lark appeared first at Port Sydney in 1887 and is an abundant breeding resident. Again Fleming (1907) lists it as a common breeding resident of Toronto. Finally, Soper (1923, p. 501) calls it a common summer resident of Wellington and Waterloo counties.

Quebec. The Prairie Horned Lark did not, apparently, penetrate to this province until long after it entered Ontario. Indeed, it seems probable that it finally entered this region by way of northern New York and Vermont rather than from the west. Dionne (1906) does not mention it as a breeding bird, but Terrill (1911) quotes Wintle's 1896 "List of Montreal Birds" as listing this Lark as a "summer resident; common". Terrill adds: "This species has been steadily on the increase

[since 1896] and I should call it an abundant summer resident." Another recent record for the southern border of Quebec is that of Mouseley (1916), who found the Prairie Horned Lark breeding at Hatley, Stanstead County, for the first time in April, 1915.

The Larks of Quebec nesting north of the Saint Lawrence River seem to be *Otocoris alpestris alpestris* (Lewis, 1921). And Townsend (1923) has recently shown that this form breeds south of the Saint Lawrence Bay on the Gaspe Peninsula. Mr. P. A. Taverner, in a letter to the writer dated June 2, 1927, gives the following information relative to the birds of the North Shore of the Gulf of Saint Lawrence and the Magdalen Islands: "*Praticola* has been generally assumed to be the Magdalen Island bird, but we have well-marked *alpestris* (apparently breeding), along with others from there that agree as well with *hoyti* as with *praticola*. Of course an intermediate between *praticola* and *alpestris*, carrying the colors of the former and the size of the latter might well be indistinguishable from *hoyti* and probably that is what these birds are. If a decision is necessary it is best perhaps to say that the birds of the Magdalens and the North shore of the Gulf of the St. Lawrence *are O. a. praticola* intergrading with *O. a. alpestris*.

New Brunswick. Moore (1903) gives the most extensive account of the first occurrence in this province. He says: "It has been known for some years that Prairie Horned Larks bred in New Brunswick as several times the old birds had been observed feeding the young." The first nest was found spring of 1902. It contained four eggs. He gives the following additional material: On Mount Keswick, May 26, 1898, a pair was observed with actions of breeding birds. On July 9, 1895, an adult Lark was noted feeding two young.

Prince Edward Island. Klugh (1921) noted the Prairie Horned Lark as "common in the fields".

Nova Scotia. Mr. R. W. Tufts, Federal Migratory Bird Officer of the Maritime Provinces, who established the first breeding record for Nova Scotia, has, most kindly, supplied me with information regarding the status of the Prairie Horned Lark in this province and others under his jurisdiction. Because of the value of this communication it will be quoted in full:

"On September 2, 1918, two Prairie Horned Larks were seen

feeding in the road near Aylesford, Kings County, Nova Scotia. One of these was taken and sent to Mr. Piers, Curator of the Provincial Museum at Halifax. My notes give the following measurements: L. 7.25′, Wing 3.92′, Tarsus 2.80′, B. from N. .36′. The bird was mounted and is still in the Provincial Museum and constitutes the first record for Nova Scotia. I regret that my notes do not state whether the specimen was male or female.

"The following subsequent records may be of interest: 1920, May 19th, one seen on the road to Yarmouth County, Nova Scotia. August 30th, three seen flying over the sandy barrens known as "Old Aldershot" between Auburn and Kingston, Kings County. 1922, May 20th, one seen at "Old Aldershot" near Auburn. June, reported by a reliable observer as breeding in the fields and pastures at Amherst, Cumberland County, Nova Scotia, a nest with eggs being reported. 1925, May 7th, saw male and female on plains at "Old Aldershot" which were unquestionably mated.

"I find in my files a letter dated June 22, 1921, from a reliable correspondent and observer (Mr. Alban Brown), living in Pictou County, Nova Scotia, which states that Prairie Horned Larks were common about his farm and adjacent fields, during the summer of 1920 until the fall of that year and 'this year (1921), they appeared the last of April while I was harrowing, and from their actions I am sure that they were preparing to nest.' Mr. Brown wrote me again on August 21, 1921, stating that two or three young Prairie Horned Larks were seen on his farm, one of which was able to fly only a short distance and was finally captured for examination and identification.

"A letter received from this correspondent a few weeks ago tells that this species has been observed continuously in Pictou County every year since, but does not appear to be increasing.

"It is my opinion that Prairie Horned Larks are now fairly well established as summer residents throughout Nova Scotia in localities which are suitable to their habits, though in no place are they abundant or even common.

"During the last four or five years I have had opportunity to cover New Brunswick frequently during the summer months, traveling by motor, and am therefore able to give you first hand data concerning the distribution of the species in question in that province. They are to be found along the north

shore in Westmoreland, Kent, Northumberland, Gloucester and Restigouche Counties, and have been noted in sections near the coast, but I have not seen them in any other counties in the province, but would expect to find them in Charlotte and Saint John Counties as well. I have just returned from a trip along the north shore in the counties first named, and saw in all only five specimens, two of these were taken in Westmoreland County, a male and a female, and dissection proved that they were mated birds.

"Within the past three or four years I have, on a number of occasions, observed Prairie Horned Larks throughout the rural districts of Prince Edward Island and they are unquestionably breeders in that province. I regret that I am not able to give you exact dates of the observations in Prince Edward Island."

Practically contemporaneous with the movement of the Prairie Horned Lark into New England as a breeding bird, appear records of its occurence in Pennsylvania; later it appeared in Maryland, and still later in West Virginia. If, as the records show, the Lark first appeared in Ontario, then in northern and western New York and from New York to New England, it is not unreasonable to suppose that New York also provided an ingress to Pennsylvania and the regions east of the Allegheny mountains.

Pennsylvania. The first record for the state is at Erie, on the lake of that name, only a few miles west of the southwest border of New York. It was reported by Sennett (1889). Todd (1891) reported this Lark in Butler County, June 10, 1889, and "probably breeding." Dwight (1892) shot a specimen of *O. a. praticola* at Athens, Bradford County, June 12, 1891 (the northeast region of the state). Bailey (1896) reported it as a common breeder in northern Elk County (north central region). Rhoads (1899) recorded it as breeding in a suburb of Pittsburgh in 1898, also in Allegheny, Beaver and Butler Counties. It is interesting to note that Brooks (1908) found a Lark breeding in Pittsburgh also (April 4, 1908), in Schenley Park* the same situation as given for the first record for the city by Rhoads ten years previously. Finally Harlow (1918)

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* This locality, Schenley Park, Pittsburgh, is, it seems, a favorite place for Prairie Horned Lark observations for Sutton (1927) makes frequent reference to Lark activities noted there.

states that the bird breeds over most of Pennsylvania north of Northampton, Schuylkill, Northumberland, Cumberland and Franklin Counties, was found nesting on the Pocono Plateau in Huntington, Center and Green Counties.

Maryland. Eifrig (1904) reports the Prairie Horned Lark as breeding in the "higher parts" of western Maryland and again (1920) speaks of it as a "not uncommon breeder" in the vicinity of Oakland, western Maryland. In neither of these cases does he say that nests were found, though in refutation of a "first" breeding record reported by Swales (see below), he says (1923) that he "has taken this race summer and winter in Allegheny and Garrett Counties since 1900, and his records of breeding (see above) "were backed by specimens taken." Swales (1922) reports an adult male and two juveniles taken at Laurel by Marshall.

District of Columbia. No breeding records were uncovered, but Smith and Palmer (1888) took *O. a. praticola* in the vicinity of Washington in February, 1881.

West Virginia. Brooks (1908) noted *O. a. praticola* in Kanawha County, June 19, 1902; "seems to be resident" in Wood County. A specimen was taken in the Poco Bottoms, Putnam County, October 15, 1902; a pair was secured at Cameron, Marshall County, June 11, 1900; noted in Lewis County in breeding season; in 1905, young were noted just from the nest near Morgantown. At French Creek, April 11, 1905, a nest with three young birds was found. Dadisman, in an account in Bird Lore (1919), says that "three years ago this summer," a pair of Prairie Horned Larks nested in Morgantown, West Virginia. The nest was seen.

Thus it seems that the Prairie Horned Lark, having entered Ontario, 1868-1873, moved next into New York and simultaneously from there into Pennsylvania on the south and New England on the east. Its southern breeding limit is West Virginia on the south, but the sea alone has stopped it from Massachusetts to the Saint Lawrence.

This assumed extension of range of the Prairie Horned Lark has not been without its critics. The first of these is Norton (1906), who asserts that Henshaw's (1884) erection of the subspecies merely directed attention toward it, and so accounts for the many recent records of the Lark where formerly

it had not been known to breed. He further claims that Audubon, in 1833, discovered the equivalent of the Prairie Horned Lark at Bras d'Or, Labrador, and figured it ("Birds of America" II, plate CC.), describing it as the nuptual plumage * of the Horned Lark in Volume 2, Ornithological Biography (1834), p. 575). Moreover, Norton goes on to say that the Prairie Horned Lark was rediscovered by the Bowdoin College Expedition in Labrador in 1891 (Proc. Portland Soc. Nat. Hist., II, p. 153). And, again, that Maynard's "Naturalist's Guide" (p. 121), published in 1870, cites a record of this subspecies for July, 1869, in eastern Massachusetts (see also above under Massachusetts). All of which, in Norton's opinion, "shows conclusively that it has not suddenly extended its range eastwardly."

Another competent ornithologist, Barrows (1912), believes this "eastward movement" invalid. He says (p. 409): "It is conceivable that the species has always occurred in small numbers throughout the northeastern states, but that it has passed unnoticed until recent years, when the increase in the number of collectors and the more general publication of field notes have called attention to its presence."

In my opinion, however, there is no question as to the validity of this extension of range. Opportunity has not been presented, as yet, to look up Audubon's illustration to which Norton (see above) calls attention, but *O. a. praticola* was eliminated as a bird of Labrador in Townsend's and Allen's "Birds of Labrador" (Bost. Soc. Nat. Hist., V. 33, No. 7, pp. 277-428, July, 1907). Furthermore, the following points seem to establish the probability of this extension of range beyond a question:

> (1) The general removal of forests throughout all the northeast has made available, within the last seventy-five years, vast areas of sterile ground admirably suited to the uses of the Lark. One has but to climb the hills of south central New York, view their rock-strewn, barren summits, from the soil of which nearly all virtue has long ago leached out, to become forcibly convinced of this

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* Even Mr. Robert Ridgway as late as 1881 considered the pale plumage of *praticola*, which he found breeding in Illinois, to be *alpestris* merely in a "much faded summer plumage".

fact. Such must also be true of much of New England, of Pennsylvania, Maryland and West Virginia.

(2) Wherever agriculture or farming is practiced, there the Prairie Horned Lark will find suitable breeding quarters in the gardens, on the plowings, in the closely-grazed pastures.

(3) The Prairie Horned Lark is possessed of a remarkable versatility in the rapid adoption of new breeding areas, as will be shown later in the study of the bird at Evanston, Ill.

(4) The keen observation of McIlwraith (see above), who gives within a year the date of the appearance of a new Lark into Ontario in a region that he had carefully worked several years prior to this time, is one of the best evidences of the extension of range. Furthermore, his observations were made *before* Henshaw erected the subspecies.

(5) The first New York records, made shortly after the observations of McIlwraith, were, in some cases, in a region that had long been studied ornithologically. And these were made *before* the publication of Henshaw's paper.

(6) The July record of 1869 in Maynard's Guide (see above), if it actually represented a breeding bird, may well have represented one of the early adventures of the Lark, a pioneer, who was followed by numerous settlers twenty to thirty years later.

(7) The orderly sequence of records from Ontario to eastern Massachusetts, from New York to West Virginia, after ornithologists everywhere were on the lookout for *Otocoris alpestris praticola*, is in itself the best evidence of the routes undertaken.

Forbush (1927) stoutly defends the idea of the eastward movement and increase of the Prairie Horned Lark. He gives as a probable reason for this extension "the fact that much of the prairie land in which it formerly bred has been settled and cultivated, and tree claims have been planted with trees, thus driving out the species from thousands of square miles in the aggregate (now wooded) in which it formerly bred."

With this the writer cannot agree, for, in the first place, the Lark probably has not lessened in numbers one whit since man entered its original home, the prairies, but has increased, seizing upon cultivated fields as recompense in great measure for loss of the smaller denuded or short grass areas of prairie —the only places where it would have bred (see further). Also, the wooded area in this original home has nothing of the extensiveness that Mr. Forbush ascribes to it, consisting for the most part of scattered lots. Further, Forbush says, "On the other hand a great region in Indiana, Ohio, New York and New England formerly heavily timbered has been more or less cleared, and the fields and pastures of the East offer suitable breeding places and a plentiful food supply for this species here." With this last the writer is in full accord; indeed, this is probably the most important reason for the northeastward movement.

It is probable that regions other than those listed above have been occupied recently by the Prairie Horned Lark as conditions within them have become suitable. Quite certainly the region from Indiana to Ohio, or at least from Indiana through Michigan, must have provided breeding conditions before the bird would have entered Ontario or New York.

Ohio. Though Jones (1903) lists *O. a. praticola* as common nearly throughout the state, yet Wheaton, in his report on the Birds of Ohio published in 1882, made no reference to a breeding Lark. Henshaw, likewise (1884), on giving the distribution of *O. a. praticola*, made no reference to Ohio. Henninger (1902) says that this Lark appeared first in middle southern Ohio Oct. 28, 1899. Dwight (1890) records a specimen from Circleville, Ohio, which may have been the one Henninger mentions. If these records constitute a reasonable estimate of the first appearance into the state, then it is unlikely that Ohio was the source which supplied Pennsylvania and western New York.

Indiana. Allen (1878) quotes David Starr Jordan in the first record noted from Indiana. Says Jordan: "Professor Brayton shot here (near Indianapolis) this morning a number of Shore Larks *(Eremophila alpestris)* and among them were two young birds, about grown. The birds usually remain here most or all of the summer, but I never knew of their breeding

so early." These birds were taken April 24, 1878. Everman (1889) says of *Otocoris alpestris praticola*, "up to 1879, very rare; since then becoming more common every year, until it is now a common resident, most abundant, however, in winter and early spring." Butler (1879) quotes Mrs. Hines as reporting the Prairie Horned Lark on the increase in DeKalb County. He further notes that none was seen in Franklin County later than February until 1886, where a definite breeding record was secured in 1891. Further, he quotes Evermann as saying it was rare in Carroll County up to 1879, but that it was a common resident there in 1886. He lists the bird as breeding as far south as Bloomington, Spearsville, Greensburg, Richmond, Brookville and Bicknell.

Michigan. Henshaw (1884) had specimens in breeding plumage from this state, as did Dwight in 1890 (Cadillac, Mich.). Cooke (1893) gives a record of a February nest at Plymouth. Wood and Frothingham (1903) record *O. a. praticola* as breeding on the plains of Ascoda County (northern Michigan), and Barrows (1912) mentions records of nests in Otsego County in 1902; in Ingham County in 1904; Port Huron, Jackson County, 1889; in Grand Rapids, 1896; and southeastern Michigan, 1895. To presume that the Lark entered Ontario from Michigan also carries the presumption that it bred first in Michigan. Since Michigan was, at one time, extensively wooded, the present general distribution in the state must have followed the cutting of the timber. This timber-cutting should, for the sake of the hypothesis, have occurred some time prior to 1873, the date of the appearance of the Prairie Horned Lark in Ontario. However that may be, it is more probable that Michigan provided entrance to Ontario than Indiana or Ohio.

Illinois. It is probable that the prairies of Illinois constituted an early home of the Prairie Horned Lark and from here the bird spread north and east. Ridgway (1878) says of *Eremophila alpestris*, Horned Lark: "Abundant in suitable localities." Henshaw (1884) and Dwight (1890) had breeding birds from this state. Dwight lists Mt. Carmel, Richland County, Adams County, Mason County, Sugar Creek Prairie, Waukegan, Calumet, Riverdale, W. Northfield and Evanston as the locations of his breeding specimens. Poling (1889) calls

it an "abundant breeder" at Quincy. Since much of this paper is concerned with the Prairie Horned Lark in northern Illinois, more will not be said of their distribution, but Forbes' (1908) records of Prairie Horned Lark numbers might well be given here. In this statistical study A. P. Gross and H. A. Ray walked, thirty yards apart, across portions of southern, central and northern Illinois, recording the birds of a fifty-yard strip. They observed 296 Prairie Horned Larks, or 3.8 per cent of the total number of birds. The Larks were seventh in order of abundance, being exceeded by Red-Winged Blackbirds, Dicksissels, Mourning Doves, Bronzed Grackles, Meadowlarks and English Sparrows.

Similar surveys made in 1909 (Forbes and Gross, 1922), differed from those of 1907 in that records were made for the three portions of the state at nearly the same dates (that is in June, July and August in each), whereas in 1907 southern Illinois was covered in June only, central Illinois in July only and northern Illinois from very late July (July 29) to early August only. The 1909 records are thus more representative. In this later survey 414 Horned Larks were seen and they assume sixth place in rank of total number seen (being preceded by Mourning Dove, Cowbird, Meadowlark, Bronzed Grackle and English Sparrow). Indicative also of the Prairie Horned Lark's breeding range is the very informative fact that, for the two years in southern Illinois, it was 25th in number (only 55 being recorded), in central Illinois it was 8th (204 birds), and in northern Illinois 5th (451 birds). Now, since the amount of ground covered in each region varied less than fifty percent, these figures show a striking preference for northern Illinois. This may give a clue to the optimum conditions for breeding of the Prairie Horned Lark. The conditions of the country, verdure and crops were strikingly similar in all the regions covered thus leading to the conclusion that general distribution in this state is a matter of life zone (temperature), and since southern Illinois is Lower Austral, central Illinois Upper Austral and northern Illinois Transitional, then the optimum for the Prairie Horned Lark is not reached until the temperatures of the Transitional zone prevail though it may breed in all three (and indeed on up into the Canadian).

However, conditions other than general life zone restrict the Lark severely in its breeding habitat, more so than with many birds, but these will be considered under "reproduction."

From Illinois it seems probable that the Lark moved into Indiana and Michigan, from Michigan to Ontario, from Ontario to New York, from New York to New England and Pennsylvania. It is possible that the route may have been by way of Ohio to western Pennsylvania, from thence to western New York and from thence to Ontario. The records incline me to the former view however. It is obvious, that the route must have been through Indiana, Michigan or Ohio.

Wisconsin. Coues (1874), tells of Larks nesting at Racine, Wisconsin. Kumlien and Hollister (1903), call it the "common resident Lark, abundant breeding bird in all suitable localities." There is no further evidence to show that it has recently occupied this state and it is probable that regions of prairie have been utilized as breeding grounds for a long time, though undoubtedly wherever it occurs in regions previously forested it must, of necessity, have come into them recently.

Missouri. The prairies of northern Missouri have been the homes of the Prairie Horned Lark for a long period but there is evidence that it here has extended its range south until it now breeds throughout the state. One of the earliest records is that of Scott (1879), who notes "*Eremophila alpestris*" as a common resident. "Found only on the Prairies, breeds." Woodruff (1908), gives a breeding record for Eudy, in Shannon County (south central part), March 23, 1907. Widmann (1907), calls this Lark a "common resident in all parts, on prairie and in Ozark clearings."

Kentucky. The Prairie Horned Lark may have reached this state from Missouri, Illinois or Indiana, regions where it has for long existed as a breeding form. However, the first apparent breeding records for Kentucky are very recent. Howell (1910), saw a pair in Midway, July 9, 1909, that were probably breeding forms and Blincoe (1925, p. 411), in his "Birds of Bardstown, Nelson County, Kentucky," describes it as a common winter bird and believes "it will be found breeding eventually."

Primitive Range.—In this extended account those regions into which the Prairie Horned Lark has penetrated, apparently within recent times, have been most carefully surveyed. The earlier home of this form and the base region from which all this recent movement extended will be more briefly noted.

Coues (1874) gave Iowa and Minnesota westward as the range of the then subspecies *leucolaema* from which *praticola* was later split off. Henshaw (1884) had specimens in breeding plumage from Minnesota and eastern Kansas (in addition to Missouri, Wisconsin, Michigan, New York and Illinois—see above). Dwight (1890) included eastern Kansas, eastern Nebraska, eastern Dakota and Manitoba with the western limit at the line when prairies cease and plains begin which "is also nearly coincident with the north and south line of twenty inches annual rain-fall." Oberholser (1902) did not include more territory on the west than did Dwight.

It is probable then that the home of the Prairie Horned Lark, prior to 1870, was restricted to that great prairie region that began with eastern Illinois, extended through Iowa, Minnesota, northern Missouri and the eastern ends of Kansas, Nebraska, South and North Dakota together with all the south half of Manitoba. Here it probably flourished in large numbers ready, as soon as the hand of man provided the proper conditions, to move out into all territory that the axe and the plow so unwittingly made suitable.

Henshaw (1884) gave as the distribution of this Lark, as already noted, the "upper Mississippi Valley and region of the Great Lakes" with specimens in breeding plumage from Minnesota, Wisconsin, Michigan, New York, Illinois, Missouri and eastern Kansas. Dwight (1890) extended this range to include Manitoba, Dakota and Nebraska, Vermont and Long Island. Oberholser (1902) further extended it to the north shore of the gulf of the Saint Lawrence (in 1918, however, he excluded this region), into the New England States through Maine and south into Pennsylvania, and at the present time there is evidence to show that *Otocoris alpestris praticola* now breeds in all the territory from the Maritime Provinces south to Maryland (excluding New Jersey and Delaware) west through West Virginia, probably through northern Kentucky, all of Missouri, eastern Kansas, north through eastern Nebraska, eastern South

Dakota, eastern North Dakota well into Manitoba; east again through Ontario to the west end of the Gulf of the St. Lawrence.

Of the origin of *Otocoris alpestris praticola* prior to its occupancy of the prairie region of central United States but little can be given at this time. The opinion of the writer is that the origin of this form must have come from a more southern Horned Lark than *alpestris, enthymia* or *hoyti.* This conclusion is based upon the remarkable physiological cycle of *praticola* that prompts breeding activities in March, long before conditions in much of its present range make such activities reasonably successful. Such activities are logically explained only on the hypothesis that *praticola* has carried north with it, too recently for natural selection to have eliminated, a breeding season suited best to more southern, less rigorous conditions. Perhaps in eastern Kansas, Missouri and Iowa a March nest is profitable and perhaps *praticola* has been there for a very long time.

This extensive account of the distribution and extension of breeding territory of *praticola* cannot be closed without referring to a condition that seems to prevail in Europe with respect to *Otocoris alpestris flava.* Gatke (1895) gives the most extensive evidence of this, based upon his lengthy observations in Heligoland. It will be necessary to quote him at some length: "There is probably no species which has so rapidly and in such numbers advanced the limits of its distribution as this Lark has done in the course of the last fifty years, and nowhere are its annually increasing migratory flocks displayed so abundantly, as at present is regularly the case in Heligoland during the autumn and spring migrations.

"Until the autumn of 1847 the Shore Lark was known here only from the examples shot by the brothers Aeuckens some ten years before that date; during the October and November of the latter year, however, the birds all of a sudden appeared in such large numbers that another gunner of the name of Aeuckens was able to shoot twenty of them in one day . . . . The numbers increased steadily every year from that time." His notes further give a range of from "several daily", 1850, to "thousands" in 1884. Gatke goes on to say: "the original home of the Shore Lark is North America . . . . By degrees

this species has advanced its nesting stations throughout the whole of northern Asia and Europe as far as Scandinavia, and there is no doubt that it will next establish itself in the north of Scotland; there might then result the most interesting fact of some of these birds flying across the Atlantic back to their original home as exceptional visitors . . . . This species must have displayed, even from its origin, a strong inclination for a westerly autumn migration, for otherwise it could never have got across into Asia and finally to Lapland and Finmark."

The above assumed extension of range is argued against at length by Naumann who twits Gätke for his notions as follows: "Anzunehmen, das die Art vor ihrer Entdeckung als Brutvogel in Lapland nicht dort genistet hätte, ist äusserst gewagt." I can find no evidence that Gatke implies that the bird did not nest in Lapland prior to its discovery there. But Naumann goes on: "wenn man den Fall *vorurteilsfrei* [italics mine] betrachtet, so verhalt es sich mit den Beweisen für Gätkes Annahme gerade wie mit denen für die fabelhafte Wanderung des Blaukehlchens und der 'Umfarbung' gewisser Vogel ohne Mauser." And then he gives Barrow's argument (see above) to disprove the extension: "Es mag ja immerhin sein, dass die Art durch ihren Bruten günstige Jahre in neuerer Zeit häufiger geworden ist aber in übrigen genügt zur Erklärung ihres vermeintlichen häufigeren Auftretens der Umstand das eben heute mehr beobachtet wird."

However that may be there are others of Gatke's mind. Saunders (1899), for instance, says that it "has undoubtedly spread westward from America in recent times and is still extending its range in that direction." With this very probable extension of range of a closely related form in Europe in a country long stabilized as to forests and cultivation, the record of *praticola* in this country becomes the easier to understand.

MIGRATION

General.—The preceding account has concerned itself, primarily, with the breeding range of the Prairie Horned Lark. The winter range, as one might expect, extends much farther south, but is, on the whole, very poorly defined. This is the result of the rather desultory, more or less random movement

of a bird that is not migratory in the full sense of the word. Unlike *Otocoris alpestris alpestris* which moves entirely from its summer range in winter, *O. a. praticola* may be found throughout the year in the southern limits of its breeding range. Whether all individuals of this subspecies move south in winter, northern forms replacing southern in southern Illinois, Missouri and Kansas and the breeding forms of these regions moving further south, or whether the birds here are permanent residents, that is sedentary, and the northern forms pass over their heads to regions further south cannot be said. Such questions can be answered only by marking or banding individuals. Whatever the case may be, individuals are never lacking, at any time of the year, throughout the southern half of the breeding area and even on the northern border representatives are rarely wanting for more than six weeks or the two months of December and January.

Henshaw (1884) notes that it occurs in Texas in winter; Dwight (1890) records it from South Carolina and central Texas; Oberholser (1902) gives the Carolinas, Kentucky, Texas and casually west to Colorado and Arizona. Smith (1912) writes that it arrives November 9 and leaves March 20 in Montgomery County, Virginia; Brumley (1893) says it was common at Raleigh, North Carolina, in December, 1885, again with *O. a. alpestris* in January, 1887, and in small numbers January, 1893. Loomis (1887) took *O. a. praticola* in Chester County, South Carolina, early December, 1886. He records (1888) great numbers in December and January; of these he collected, in December, 119 of which 103 were females and only sixteen males. In January he collected thirty females and only ten males. This amazing discrepancy in sex is a phenomenon of migration the explanation for which is not clear unless it be that the males, more attached to their breeding territories, remain nearer to them, or begin their return to them much earlier than the females. Loomis (1891) continued these observations with similar results. He notes, in addition to the discrepancy of sex (42 males, 225 females in birds shot in 1887, 1888 and 1890), that the first arrivals appear the last week in November.

Wilson (1922) calls the Prairie Horned Lark a common winter resident at Bowling Green, Kentucky, noted from July 28

to May 11. Cooke (1908) took *praticola* in Georgia (Clayton County, November 30, 1907). Isley (1912) tells of this subspecies in Sedgwick County, Kansas (middle south region). Cooke (1914) in recounting the winter birds of 1883-4 at Caddo, Oklahoma, remarks, concerning the Prairie Horned Lark, that it appeared in large flocks October 26, remained constantly and in numbers to January, decreased from then to February 18; none on February 20; a few in pairs March 8. Lastly, among those records of birds wintering south of their breeding range, is that of Attwater (1892) who calls *O. a. praticola* a common winter resident of San Antonio, Texas.

As previously noted, the Prairie Horned Lark is absent as a species for a period of about six weeks to two months in the winter toward the northern limits of its breeding range. The last noted in 1925 at Evanston, Ill., was a single individual on November 27, the first returned January 10, 1926. The migration dates for Ithaca, N. Y., from 1908 to 1921, are as follows:

Year	First Seen	Became Common	Last Seen
1907	Feb. 17	Feb. 24	Nov. 19
1908	Jan. 22	Feb. 23	Nov. 3
1909	Jan. 9	Feb. 12	Nov. 7
1911	Feb. 9	Feb. 9	
1912	Jan. 28	Mar. 7	Oct. 18
1913	Jan. 26	Feb. 19	Oct. 26
1914	Jan. 6	Feb. 14	Dec. 8
1915	Jan. 26	Feb. 18	
1916	Jan. 16	Feb. 20	
1917	Jan. 8		Nov. 28
1919	Jan. 18		Nov. 15
1920	Jan. 8	Feb. 29	Nov. 6
1921	Feb. 8	Feb. 21	Oct. 30
Average	Jan. 23	Feb. 21	Nov. 9

Mouseley (1916) gives March 15 as the average date of arrival (for four years) at Hatley, Stanstead County, Quebec. He mentions (1924) a "last" record on November 26 "three weeks later than any previous date." Scott (1884) mentions the 15th or 20th of February for Ottawa, at Belleville, February 9 or 10, for "*Eremophila alpestris*". Eifrig (1911) gives as early as February 10 for Ottawa, latest November 22, 1908. Soper

(1923) says that it "reaches us in late February or early March . . . . leaves about November 10," in Wellington and Waterloo Counties, Ontario. Barrows (1912) writes that it is ordinarily entirely absent from the state (Michigan) during December and January. Finally Criddle (1922) gives the following dates for Aweme, Manitoba, the most extensive observations, apparently, ever made of the migration of this subspecies:

Spring migration (Aweme, Manitoba)

Number of years	Average first date	Earliest
25	Feb. 21	Feb. 9, 1918

Fall migration (Aweme, Manitoba)

Number of years	Average date last observed	Latest
24	Nov. 14	Nov. 23, 1917

Summary of general migration.—The Prairie Horned Lark is not extensively migratory, belonging, in the categories of migration, between a form such as *O. a. alpestris* which moves entirely from its summer home for a long period and the almost sedentary species such as *O. a. giraudi* which is said to be found throughout its breeding range during the entire year. The southern limit of the winter range of *praticola* is South Carolina (occasional in Georgia), and Texas, and at this limit the bird occurs in December and January. Many spend these two months also in Kansas, Oklahoma, very probably in Missouri and in Kentucky. From middle to late November into late January or early February *Otocoris alpestris praticola* is absent from New England (Vermont, Parkhill, 1889), New York, Quebec, Ontario, Michigan, Indiana (Butler, 1897, who says December first to January twenty-fifth usually) and Manitoba. The situation is, undoubtedly, the same for all other territories, of similar latitude, where the Prairie Horned Lark breeds.

Migration of sexes and individuals.—But little can be said at this time, as to the arrival of sexes, of mature and immature birds and of resident and non-resident individuals in any given locality. If all these forms were characterized by diverse plumage as the Red-winged Blackbird (see Allen's, 1911-13, most excellent account of the migration of this form), the problem would have greater possibilities of solution. But since mature and immature birds in spring have no distinguishing characteristics in the field, and since sexes can be distinguished only

when closely approached, the only method whereby an adequate knowledge of the details of migration could be obtained would be that of extensive collecting and sexing of many birds through several spring and fall seasons. No attempt has been made, as yet, in that direction.

However, some general observations have been made in this regard. First of all it seemed evident that the first birds that arrived, both at Evanston, Ill., and at Ithaca, New York, were *resident* males. Though this is not in accord with Allen's (1911-13, p. 77) observation of the Red-winged Blackbird, still it seems strongly conclusive in the case of the Prairie Horned Lark because of the following facts: (1) the first Larks to arrive at Evanston (January 10), were not in flocks but distributed themselves singly (one pair was noted) over the breeding area; (2) full ground songs and one typical flight song were noted January 12 and much fighting was in progress between males. The same observations were essentially true at Ithaca, New York, the spring of 1927. The first Lark noted at this place was a single individual observed by Dr. A. A. Allen, February 3. The first Larks appeared on the breeding grounds February 9 and, when first observed, were scattered over it singly, singing or indulging in aerial combats.

Resident females are, it appears, the next to arrive. Some of them come very shortly after the males. Though Criddle (1917) writes that the males precede the females by two weeks at Aweme, Manitoba, I believe some females come with the first males or very shortly thereafter. What seemed to be a mated pair was noted with the first Larks, January 10, 1926, at Evanston, and *several pairs* were noted January 16, though unmated males seemed to be as numerous as mated on January 23. However there were males only on the territory February 5, but two days later paired Larks were numerous and mating activities in full swing. At Ithaca, New York, 1927, the first birds to appear on the breeding grounds (February 9), seemed to be males only but a mated pair was noted February 19, as well as one unmated male.

Transients or migrants, i. e. birds still in flocks and flying over, perhaps to more northerly breeding grounds, are frequently noted in late February and in March at Ithaca, New York. Thus on March 12, 1916, a flock of one-hundred was noted; similarly,

on February 21, 1927, a flock of about the same number was seen by Dr. A. A. Allen. It is quite possible that these flocks may represent resident birds, however, for on February 21, 1927, nearly a foot of soft snow was on the ground and this flocking may have been a secondary reuniting of resident birds forced, temporarily, from their territories. Jones (1910), has noted that the Prairie Horned Lark reflocks after mating in the spring if severe weather modifies its breeding areas. The present writer noted that prolonged and deep snow at the end of March, even after nests had been started, caused the birds to desert their territories and to collect in groups along the roadsides at Evanston, Illinois. Even though this may account for some flocks in February and March it remains true also that Larks must pass over to reach breeding areas to the north and these very probably do so in February and March after residents are established. Small flocks were noted at Evanston February 28, 1926, long after residents had come onto their breeding grounds, similarly a small flock of ten to twelve birds was flushed from a patch of *Setaria* at Ithaca, March 1. Again small flocks were noted once or twice in April at Evanston but these proved to be *O. a. alpestris* and not *praticola* (for which see under account of birds that fed over or on the subdivisions at Evanston, Illinois).

Vagrants, immature or unmated birds appeared occasionally at Ithaca, New York in April, but since the mated males drove them out of the vicinity whenever they attempted to alight, it was impossible to ascertain their sex. It is possible, though improbable, that they represented young of successful March nestings.

Summary of migration of sexes and individuals.—The following very tentative categories of spring arrivals may be listed in summary in the order of their arrival:

1. Resident adult males
2. Resident adult females
3. Transient males and females
4. Vagrant, immature, etc.

THE LARK IN AUTUMN AND IN WINTER

Under migration something has been said of the movements of the Prairie Horned Lark in late fall, in winter and early spring, in various portions of its range. There remains yet a short discussion of what may be known of its other activities at this season: its flocking, its food, its associates, and, especially, its habitats.

Flocking.—Young of early broods begin to gather in small groups in late spring and early summer long before the adults have ceased breeding activities. Thus small bands of juveniles were seen at Evanston, June 19, 1925. In 1926 at Evanston the first flocking of adults was noted on July 31. At Murdock, Nebraska, August 24, 1926, a large flock was discovered scattered out over a large tract of recently plowed ground. In September, at Murdock, Larks were frequently heard in the air and one essayed a flight song September 6. In October and November, 1925, at Evanston the only Larks seen were casual groups of twos and threes on or above the breeding grounds west of the city. They were noted thus October 25, 31, November 8, 21 and 27. At Ithaca, New York, during the fall of 1926, Larks were heard frequently flying over the Campus of Cornell University and Dr. A. A. Allen and Mr. M. D. Pirnie reported a typical flight song on November 6. The appearance of this bird in the Carolinas, Kentucky, Oklahoma and Texas during December and January has been discussed under migration and its reappearance in the latitude of northern Illinois (Evanston) and south central New York (Ithaca) has also been considered.

Habitats.—The conditions preferred by young or by adults in fall or winter do not differ materially from those in which the species breeds. These conditions are those of the open field and areas in which a minimum of vegetation prevails. The close-cropped pastures, the great fields of fall plowing in the Missouri Valley, closely mowed cemeteries (Evanston, July 31, 1926) are examples of conditions in which Prairie Horned Larks have been found at these seasons. Though the surveys of Forbes and Gross (1922) were made in early and late summer they do not differentiate between breeding and non-breeding birds so these records will be considered here. They show the Prairie

Horned Lark as the dominant form of plowed ground bird and show, as well, that more were found in such conditions (162 individuals of a total of 710) than in any other. The next most favored habitats they list are pastures, then wheat, rye and barley fields, then meadows, then corn (of early summer undoubtedly with much bare ground between rows), then stubble, then oats, with but a single record from waste and fallow ground (very probably because it is weed grown at this season). As might be expected not a Lark was recorded from woods, orchards, shrubbery or swamps. The young Larks especially show their inherited taste for the bare, verdure-wanting localities and in these they will be found in June and July while their parents, forced by the exigencies of second and third broods and the inability to move nests from the flora that grows rapidly about them, are forced to spend much time in conditions they would not naturally favor. The young at that time are a more proper index of the optimum habitat of the Prairie Horned Lark. Loomis (1891) is one of the few who describes the conditions in which wintering flocks are found in the south. These, in South Carolina, are barren upland pastures where grass has been cropped to the roots, wind-swept grain fields, cotton fields where stalks are small and the ground free from grass. As birds of the barrens one would not expect Larks to alight in trees freely, nor on wires. Indeed Sutton (1927) says "I have never seen one alight on any leafy bough, bush or wire". Such is generally true, but Mouseley (1916) remarks the Larks of a breeding pair alighting in a tree before approaching the nest, and the writer has seen the singing males at both Evanston and Ithaca frequently on posts, stakes and building tops and the "B" male now and then alighted, insecurely, on a smooth wire stretched above the garden at Ithaca. Eifrig (1902) reports Prairie Horned Larks coming into the city streets in Maryland and there eating with the House Sparrows when snow covered their normal food supply. Those incongruous homes, the icy, boreal-blasted fields to which the Prairie Horned Lark returns in January and on which he begins his songs, though the temperature may be zero, are a part of the breeding season and under that they will be considered.

Associates in fall and winter.—The Prairie Horned Lark is essentially alone in his choice of habitats in the breeding season, none other approaches the desolate ecological niche in which he

is content; but in winter birds from farther north, from Arctic tundras and barrens, share with him his favorite flocking grounds. Thus Brimley (1893) reports Prairie Horned Larks associating with Horned Larks at Raleigh, North Carolina. At Evanston also the Horned Lark found the home of *praticola* suitable for a temporary abode and great flocks of Lapland Longspurs ran about on the barren flats apparently as much a part of that environment as the Larks themselves.

Nightly quarters.—Apparently the Larks remain where night finds them on the open areas. No endeavor is exercised to locate any shelter other than that of sparse grass clump or available clod. Nor do they cluster tightly but pass the night in the same scattered groupings that they maintain while feeding. Sutton (1927, p. 132) describes the awakening of a flock wherein the "creatures left their roosts beside or beneath little clumps of grass". After a heavy snow at Evanston, Illinois, I have noted virgin morning tracks of Larks emerging from the shelter of scant grass clumps where the snow had made roofed shelters for them.

Food in fall, winter, and early spring.—McAtee (1905), in his extensive account of the food of the Horned Larks, writes that in August and September many grasshoppers are taken (7.1 and 8.9 per cent of the total food respectively), and that weevils constitute 18 per cent of the food in August. He says further that spiders are taken in every month. The conspicuous weed seeds which he lists (foxtail grasses, smart weeds, bind weeds, amaranth, pigweeds, purslane, ragweed, crab and barn grasses), are probably largely consumed in fall, winter and early spring. The total of 79.4 per cent of vegetable matter taken in the year, as given by McAtee, is made up largely of these weed seeds. McAtee found about 40 per cent of food taken in August to be animal matter, 20 per cent animal matter in September, between 10 and 20 per cent in October, 5 per cent or less in November, about 2 per cent in December, 1.73 per cent in January and 3.11 per cent in February. The animal matter of January and February consisted principally of weevils and cocoons of Tineid Moths. Grain (chiefly waste oats, corn and wheat) formed 12.2 per cent of the food of Larks (exclusive of California forms) and much of this would have been taken in the period under consideration.

The Main Subdivision at Evanston, where the most extensive observations were made by the present writer, had, in the winter of 1925-26, great quantities of *Agropyron repens* (quack grass), *Setaria* (foxtail) and *Amaranthus* (pigweed) all of which had been allowed to mature seeds. Of this the seeds of the quack grass were eaten first and wherever their long stems had fallen over the sidewalks the Larks would invariably be found in January and February. When quack grass failed, foxtail was eaten, and lastly *Amaranthus* substituted when no other seeds were available. Plate IV, Fig. 1, is a photograph showing results of Lark activities about a clump of *Amaranthus* after a March snowstorm. Once or twice Larks were noted along the roads feeding on the oats of horse droppings, when snow covered up all the weed seed of the subdivision. And again at Ithaca the compost heaps, put out for fertilizer along the garden margins, supplied some food when snow lay deeply over the ground.

At Ithaca, during the spring of 1927, Prairie Horned Larks were observed feeding on *Setaria* (March 1), on *Ambrosia artemisiaefolia* April 1; a pair of Larks were frightened away from an Arctiid moth larva *(Apantisis arge)* which I observed the female dig up, March 3. Finally a few adults were collected in March at Ithaca (Connecticut Hill) and examination of stomach contents gave the following results:

1. Female, March 6, collected about 6:00 P. M.
   - Vegetable matter 98%
     - Oats (two grains) 10%
     - *Setaria lutescens* (72 seeds) 88%
   - Animal matter 2%
     - 2 bits of feather 1%
     - Snout beetle (one) 1%

2. Female, March 11, collected about noon.
   - Vegetable matter 95%
     - Buckwheat (one whole grain and many fragments) 90%
     - *Polygonum persicaria* (four seeds) 5%
   - Inert matter (sand) 5%

3. Male, March 11, collected about noon.
   - Vegetable matter 100%
     - Oats (one grain) 5%
     - *Setaria*, two species (46 seeds) 95%

4. Male, March 11, collected about noon.
   - Vegetable matter 100%
     - Buckwheat (fragments of grains) 10%
     - *Setaria* (30 seeds) 90%

5. **Male, March 11.**

Vegetable matter 100%
***Ambrosia artemisiaefolia* (three seeds)..30%**
***Setaria* (eight seeds).....70%**

6. **Male, March 11.**

Vegetable matter 100%
***Ambrosia artemisiaefolia* (six seeds)...50%**
***Setaria*, two species (seven seeds).....50%**

In summary of the feeding habits of the Prairie Horned Lark in autumn, winter and early spring, all that need be said is that the bulk of food taken is that of seeds of weeds, and the animal food, a much smaller per cent, is almost entirely of those forms which are harmful to the agriculturist. The Lark, in feeding habits, finds for his food those things that appertain to the waste lands that he inhabits.

Call notes.—The Horned Lark, like the Goldfinch, usually advertises himself in flight by a definite, unmistakable note. Excepting an occasional song, this is about the only sound from the birds in fall and winter. Reed (1923) describes this flight note as "tseet" and Knight (1908, p. 325) puts it into such words as "we-tseet" or "weechy-weer".

The flight and call notes are several in number however, some of them appertaining more especially to the breeding season than to wintering birds and in that connection they will be considered again. The chief stock in trade of the Lark and the one most commonly heard is "p-seet" or merely "zeet". It is uttered casually on the climb of the ordinary undulating flight, especially on long journeys and in flights of young birds. Adults frequently make low flights over the ground without uttering a note. This "p-seet" is occasionally, sometimes frequently, lengthened to "p-seet-it" during the flight. When flushed the note is "zu-weet" or "zur-reet" (long drawn), "zeet-eet-it", or "zeet-it-a-weet", which is so high-pitched and mournful in character that it makes the birds indeed a part of the winter's gale that whips them away.

Flights.—Breeding birds, such as females in abandonment concealment of the nest, or males in flight song, exhibit several distinct flights, but at other seasons the flight is of but one definite character. This is a choppy undulation brought about by three or four rapid, even strokes of the wings interrupted by the space of about two beats during which the wings are closed.

The note is uttered on the climb of each undulation. Or again on prolonged flights the character of the wing beats is as follows: Long strokes are made, one, two, three (or one, or one, two), with a pause of about one wing beat between each stroke wherein the wings are folded. Then come four to six rapid and successive strokes which cause a climb. At this time the note, "zeet-it" is uttered. Then comes a pause of the length of one or two beats, with wings folded, causing a drop in elevation. These repeat. The bird goes thus: jump, jump, jump, climb (call also), drop, jump, jump, jump.

REPRODUCTION

Breeding Habitats

General.—Other writers give the following habitats for the nestings of the Prairie Horned Lark: On ridges of corn (Isley, 1912, Kansas); beside hills of corn (Crone, 1889, Iowa); meadow-highland and cornfields (Jones in Davie's "Nest and Eggs of N. A. Birds", 1889, Iowa); first nest in closely cropped pastures, June nests at the hills of corn (Hess, 1910, Illinois); grass-sparse uplands, not prairie (Criddle, 1917, Manitoba); between the end of ties of the Canadian Pacific Railroad (J. F., 1900, Ontario); in old meadows (Eifrig, 1911, Ottawa); on ploughed fields (Soper, 1923, Ontario); inside of manure heap in a field (Davison, 1885, New York); fallow fields, prairie tracts, pastures, country roads (Bendire, 1895, general); early nests in meadows and pastures, later in potato and cabbage fields (G. E. Harris account in Bendire, 1895, New York); in the oval of a race track in Schenley Park (Brooks, 1908, Pittsburgh, Pennsylvania); in the middle of a golf course (Burleigh, 1923, Pennsylvania); dry undulating field, ground more or less covered with snow, in bed of hair-cap moss, another in a damp meadow (Mouseley, 1916, Stanstead County, Quebec); in a sheep pasture on top of mountain, very unprotected (Brewster, 1894, Massachusetts); in an old plowed field too wet to sow (Swain, 1900, Maine); in fields and pastures, sandy barrens (Tufts, letter of June 21, 1927, Nova Scotia), in a field of young oats drilled into a former corn field (Forbes and Gross, 1922, Illinois).

That the other subspecies of *Otocoris alpestris* select the verdure-denuded opens can also be shown by a few references: dry and bare ridges in a wet meadow (Merrill, 1888, *O. a. strigata*

in Oregon); bleak and barren . . . plains (Batchelder, 1885, *O. a. chrysolaema* in New Mexico); in park-like openings in the mountain forests up to an altitude of 10,000 feet (Mearns, 1890, *O. a. adusta* in Arizona); on bleakest and most exposed hillsides (Bigelow, 1902, *O. a. alpestris* in Labrador); on prairies, in denser vegetation than *O. a. praticola* (Criddle, 1917, *O. a. enthymia* in Manitoba).

In summary of these accounts three or four things are to be pointed out: (1) the Prairie Horned Lark selects the bleakest barrens available in every locality in which to nest. These may become weed grown during the nesting but the optimum condition, the criterion of the Lark's choice, is the condition of these localities when the site is selected and the nest built; (2) the "barren" condition is, apparently, that which possesses little or no verdure. Moisture, elevations, nature of soil, are all subservient to that one requirement—bare ground; (3) from the close-cropped pasture (an ideal "barren" in March), the Larks are driven by press of verdure in May; then they select the last bare ground available—the gardens, the cultivated fields; (4) all other subspecies of the Horned Lark seem to resemble the Prairie Horned Lark in their selection of nesting sites though *O. a. praticola,* exceedingly versatile, has invaded those "barrens" that civilized man so artificially creates.

The breeding territory at Evanston.—About one and one-half miles from the west limits of the city of Evanston, Illinois, and about two and one-half miles north of the north bounds of Chicago, lies the bit of territory which was worked most thoroughly in this study. This, like many hundreds of acres on all sides of it, was, until a few years ago, an extensive marsh. At that time it was, manifestly, unsuited as breeding grounds for the Prairie Horned Lark.

Portions of this marshy area were, with difficulty, put under cultivation after a drainage canal had partially removed the water, but much remained unutilized and weed-grown. That area, which later became what is called the "Main Subdivision" in this paper, was one of these weed-grown regions and a smaller area just west, here called the "West Subdivision", was put into gardens. Here it is well to call attention to the fact that, though the Larks might have nested in the gardens of the West Subdivision, they could not have nested in the Main Subdivision

until the time of the changes about to be related. That they came onto this area in great numbers within two years after its conversion is but another evidence of the striking versatility of the Prairie Horned Lark in acquiring new breeding territory.

The weed-grown condition of the one area remained unmodified until 1923 or 1924, at which time the entire surface, very flat previously, was altered to form a golf course. Drainage was completed, artificial hazards created, bunkers, greens established, mounds were thrown up here and there. Though the area was not under close observation at that time it is quite possible that a few Larks may have nested on the margins of the sand hazards as they do on many golf courses in their range.

The golf course was short-lived. In the fall of 1924 a branch of the Chicago Elevated Railroad penetrated to the vicinity. Promptly the erstwhile golf course was subdivided; sidewalks stretched themselves out over night, whirling lot-sale signs clattered everywhere and those indefatigable, hopeful pillars of progress, the street sign posts, soon stood like solitary glistening martinets on the otherwise uninterrupted landscape.

But this, the Main Subdivision, became a paradise to the Prairie Horned Lark. In the spring of 1925 the grass of the former course was burned off and the whole subdivision presented a blank, black, almost smoothly denuded face. Here the Lark was at home. Even in June, in areas in which vegetation came on slowly because of scraping or sanding for former hazards, nesting was still in progress. During the summer of 1925 sewers were laid in the street-ways, north and south, and this activity threw up a mound of dirt thirty to forty feet wide in the center of the street, a strip that grew no verdure until late summer, 1926. And so, at its edge, in the thin grass strip between it and the sidewalk there were provided sites for fifteen located nests of the Prairie Horned Lark (see Fig. 9; Plate III, Fig. 1; Plate XII, Fig. 1; Plate XIII, Figs. 1 and 2), during 1926.

In 1926 the Main Subdivision began the nesting season with closely clipped, dread grass of *Agrostis palustris* (red-top), and *Poa pratensis* (blue grass), with here and there, in old hazards, coarse stems of dead thistle *(Cirsium arvense)*, primrose *(Oenothera biennis)*, ragweed *(Ambrosia artemisiaefolia)*, white, sweet clover *(Melilotus alba)*. Much of the ground though, was bare

and black where the grass had been burned off. Throughout April the only verdure was the green tips of new grass but in May the dandelion *(Taraxacum officinale)* made all the area a great field of yellow; dandelion gave way to blue grass in June; blue grass to red-top; and by July the whole surface, even most of the streetways, were grown up in heavy verdure. As the plant life grew the Larks were forced first from their nest sites within the blocks, secondarily from their narrow strip near the street mounds and lastly, in late June, even from the hazards whose depressions, stripped and sanded, nevertheless, under the influence of the summer sun, produced too much vegetation for the Larks. But what was inhospitable to the Prairie Horned Lark proved the most acceptable home to many another bird.

The West Subdivision (bordering the Main Subdivision on the west), as previously stated, had been a garden plot for some time but it, too, suffered subdivision, though not until the spring of 1926. Having had no grass, and having been cultivated the year before, the weeds grew slowly in 1926 and here, among the scattered clumps of wild mustard, bindweed, lamb's quarter, cocklebur, wild lettuce and thistles, on the last bare ground the vicinity offered, the July nests of the Lark were found.

The breeding territory at Ithaca.—One nest was located on the overturned sod of a former meadow (see Plate X, Figs. 1 and 2). This nest was destroyed by cultivation and the first attempt at renesting was destroyed by oat-sowing, but it is probable that one nesting may have been successful during the weeks the oats were getting under way.

The most extensive study was made of a series of nestings, just east of Ithaca, on an uneven tract that was in part devoted to gardening and in part to fall wheat and fall rye. The fall wheat area remained suitable for nesting from March, through April and well into May, though by the middle of May the wheat and rye had attained such a height that only the urge of nestlings would have kept the Larks in it. By June one pair of Larks had gone from the wheat area entirely and the other two pairs no longer occupied the portions of their territories that formerly had extended onto it, but restricted themselves to the bare areas of the garden (see Figures 2, 3 and 4).

Song

Season of song.—The extent of the season of song is a subject upon which there is little or nothing in the literature. I have before me only the following records that give dates of the beginning of song: Isley (1912), Sedgwick County, Kansas, writes that they begin to sing about the middle of January; Langille (1912) gives "as early as the last days of February"; Knight (1908, Maine) writes that the "male bird begins to sing in late March or early April"; Chapman (1923, quoting Seton) gives "springtime while the snow is yet upon the ground". Criddle (1920) reports "males singing everywhere", July 14, Manitoba. The following "late" record is by Seton (1908) for the subspecies *O. a. hoyti,* which was in full song on the Barrens in the Great Slave Lake region, August 29, 1907.

As previously noted, the first Larks returned to the breeding grounds at Evanston, January 10, 1926; the first song (from the ground) was heard January 12 while a stiff gale blew out of the northwest and the mercury was near zero; the first flight song was noted January 16 and extensive song activity was in progress from that day on, except in the most severe weather conditions. The last song in 1925 was on July 4 (both ground and flight songs), the last flight song in 1926 was on July 3; on July 14, a short ground song concluded the season. It should be noted here that songs diminished gradually and ceased altogether fully two weeks before nesting duties had been brought to a conclusion. Flight songs were noted September 8 and November 6 but had no relation to the breeding season, naturally.

At Ithaca the first songs (flight and ground) occurred on February 19, the last of the season on June 25, 1927.

There is probably no other Passerine bird that can equal this record. What an urge it must be that starts these birds off on their snow-covered, wind-swept, zero-cold barrens in January, and keeps them at it through March squalls, April showers, May storms, June sun and on into July heat, day after day, hour after hour, from matins to vespers, from month to month!

Monthly variations in song numbers.—It is possible only in a very general way to state how the relative number of songs varied from month to month. In the case of ground songs statistics are, quite obviously, impossible for an entire season for

there is no clear beginning nor ending to a song upon the ground unless one counts each rendering of the intermittent ditty, and all songs are not of this type. However a reasonably careful tabulation of all flight songs was made on every visit both at Evanston and at Ithaca. Now if we consider that the average length of a visit was the same in all months and if each month is properly weighted and averaged according to the number of visits, then at least relative figures may be obtained for the entire season. Thus of five January visits one flight song was observed, a percentage of .200 flight songs per visit. Similarly, in February, fourteen visits were made and six flight songs noted, a percentage of .428 flight songs per visit. Using this as a method of estimating amount of flight songs throughout the months of song we have the following tabulation:

Average number of flight songs noted per visit from January to July

January	.200 per cent
February	.428 "
March	1.040 "
April	1.520 "
May	2.022 "
June	1.788 "
July	.142 "

These figures are exceedingly conservative as far as total number of songs may be concerned but they are pretty close to the truth as far as percentages are concerned. May is the optimum beyond question. May is probably the optimum in all respects as far as the entire breeding season is concerned (see below under enemies of young). June, as given here, may be a little too high for more time was spent per trip during this month than during other months. But even as given it shows the dropping off in flight song in this month, a dropping off which, in July, becomes very great indeed. Incidentally the total number of recorded flight songs was 287.

There is, of course, a variation in songs dependent upon weather conditions. Fewer songs are sung when the weather is bitterly cold, especially if the day is also dark, though I have watched these birds, in February and March, climb into a stiff northwest gale, when the thermometer registered many degrees

below freezing, and for several minutes fight Boreas above that they might release the terrific energy that impelled them to song. Violent winds, on the whole, whether cold or mild, checked aerial song though rarely inhibited it altogether. Quiet, clear days were made much of but flight songs were as frequent, perhaps more so, when light clouds overcast the sky. Observations were made and records obtained on all of these points but opportunity has not presented itself, as yet, to reduce them to definite tables.

Variations in song through a nesting period.—Here again no definite statistics can be produced to show the relative number of songs of the male during the period when eggs were in the nest as contrasted to the period when young were in the nest. The chief difficulty lay in the fact that, in flight songs for instance, it was impossible to identify the individual. Also, both at Evanston and at Ithaca, there were nests with young, as well as nests with eggs, in the same region at almost all times during the breeding period, so that the total number of songs was not materially influenced by the condition at any one nest. Some general observations indicated that the period of most vigorous song was that of nest building, egg laying and incubation and, since the male assisted in feeding the young, the period of least singing was that when young were in the nest. For evidence of this compare the table of activities of the male when eggs were in the nest (Table 15) with the activities of the male when young were in the nest (Table 17). This latter male did no singing from the ground that was noted and indulged in but one or two flight songs as far as could be ascertained.

Variations in song throughout a day.—By referring to Table 15 it can be seen that ground songs are distributed with remarkable regularity throughout the entire day, but there is some evidence in this table and from other observations that a majority of the flight songs came toward noon, and again near sundown, though they were delivered at other times as well. It is with regret that I acknowledge insufficient data also on this point. Part of the difficulty is that the majority of visits were made, of necessity, in late afternoon.

The relation of the song of the Lark to that of other birds.—How the Lark compared with the morning chorus in time of opening his song and with what company he closed his choral efforts is a matter of considerable interest. Observations made

on two or three very early morning trips to the breeding areas showed that most of the other residents preceded the Lark in song, apparently because the day must be started with a flight song and for this some light is necessary. Thus the Purple Martins on June 16, 1925, were chattering in the air by 3:20 A. M., a full-throated Robin song at 3:30; a Song Sparrow at 3:55; then the songs of Meadowlark, Dicsissel, Bobolink, Grasshopper and Savannah Sparrows before, at 4:00 A. M., the first Prairie Horned Lark rose in flight song. But even then he was invisible because of the poor light and he had beat the Bobolinks into the air.

The following notes, made in the field, about mid-June, 1926, at Evanston, are indicative of the manner of the close of songs in the evening:

7:19 P. M. Sun has set.

7:20 P. M. The sun, from below the horizon, glints upon a Lark in high flight song.

7:35 P. M. Larks are still chasing each other boisterously over the meadow, calling and singing short ditties from the ground.

7:51 P. M. Larks are now in song over all the meadow but I believe none are flight songs; too dark to be positive.

7:56 P. M. Evening star is visible just above the point where the sun has set. A coolness pervades the air.

8:00 P. M. Several Larks and a Grasshopper Sparrow are still in song.

8:04 P. M. Many stars visible. Two Larks are still singing.

At 8:10 P. M. The last song note was heard and that after a hush had fallen upon the jubilant meadow. That last note was the drowsy "pit-wit, wee, wee-pit", of the Prairie Horned Lark.

On rare occasions a Grasshopper Sparrow might start up from the beginning of slumber to give his insect trill after the Larks had ceased but the grand finale of the evening chorus belonged to the Larks beyond question, both at Evanston and at Ithaca.

Descriptions of song.—The flight song of *Otocoris alpestris praticola* is a true Lark song and in its method of delivery, at least, has several points in common with that of the Skylark of Europe. It is such an astounding exhibition on the whole, that it is surprising that more extensive descriptions are not to be found in the literature. The songs from the ground too, are

worthy of note, but until now they have never been carefully described or transcribed fully into words.

Wilson (1831) wrote of *O. a. alpestris* "They are said to sing well, mounting in the air in the manner of the Skylark of Europe . . .". Audubon heard this same bird in Labrador and gives the following description: "The male bird sings sweetly while on the wing, although its song is comparatively short. It springs from the moss or naked rock obliquely, for about forty yards, begins and ends its madrigal, then performs a few irregular evolutions, and returns to the ground. There also it sings, but less frequently and with less fullness. Its call note is quite mellow and altered at times in ventriloqual manner, so different, as to seem like that of another species." As will be shown later the Prairie Horned Lark sings for several minutes while in the air, flies much higher than forty yards and returns to the ground by one long straight drop. But *O. a. alpestris* may be quite different from *O. a. praticola* in this respect for recently (1926) Demille described the song of *O. a. alpestris* on the Gaspe peninsula thus: "The male flies straight upward for fifty or a hundred feet as the song begins, flutters a second as he hangs suspended and drops suddenly to the ground with the song's conclusion". These two descriptions are at considerable variance with the song of the Prairie Horned Lark as will be evident shortly.

Ornithologists so intent on robbing a bird of its eggs or upon collecting the bird itself could scarcely be expected to listen attentively to the song of that bird, so it is not surprising that the first adequate description of the song of the Lark should come from the Rev. J. Hibbert Langille near the close of the 19th century (1892). Though he spoke of "*Eremophila alpestris*" his bird was undoubtedly the Prairie Horned Lark. His description is, in part, as follows: "Presently I caught the way of the sound, and lo! its author was soaring high in the air, moving in short curves up, up, singing for a few minutes as it sailed with expanded wings before each flitting curve upward, till it became a mere speck in the zenith, and finally I could scarcely tell whether I saw it or not. But I still heard the song . . . one is tempted to compare it with the squeaking of an ungreased wheelbarrow. 'Quit, quit, quit, you silly rig and get away', it seems to say: the first three or four syllables being

slowly and distinctly uttered, and the rest somewhat hurriedly run together . . . This ditty sweetens on occasion . . . The black speck unmistakably reappears, and it gradually enlarges as the bird approaches. Down, down it comes, meteor-like, with wings almost closed, until one fears it will dash out its life on the earth. But no, it alights in safety . . .''

Hatch (1892), shortly after Langille's account, gives the following (also in part): ''. . . a male flitted up from the ground about ten to fifteen feet into the air and about thirty yards directly in front of me, simultaneously bursting into song . . . flitting, sailing, singing, he zigzagged right and left, mounting constantly higher and higher . . . until he entirely disappeared from unaided vision . . . Still the music . . . was distinctly audible when, after several minutes, his song suddenly ceased he closed his wings and, head straight downward, descended with the velocity of a spent bullet until, within a single yard of the ground . . . he opened his wings and touched the ground as lightly as a snowflake. . .''

Before taking up accounts of other writers I should like to point out one or two details in these descriptions at variance with my observations of nearly three hundred flight songs. (1) The Lark only occasionally seems to go higher after it begins to sing, most frequently it loses elevation for the song is, ordinarily, begun at the maximum height. (2) Only once did I observe a Lark begin to sing as he *started* to climb, as Hatch's description reads.

Hegner (1899) gives a description of the flight song similar to the above, adds that the Lark ''arose at an angle of 45 degrees, in short stretches . . . Made circles 300 yards in diameter, sang fully five minutes.'' Allen (1923) gives also a careful description of the flight song. Goss (1891), Bailey (1908) and Chapman (1923) mention the flight song though they give no careful description. Chapman, quoting Seton, also says: ''but it often utters this same song while perched on some clod or stone especially just before dawn and after sunset. . .''

Types of song.—Though Langille's description of the song, ''quit, quit, quit you silly rig and get away'', is remarkably close to one type, still he is the only writer who attempts such a description and it is of but part of the song. Bailey calls it

"quaint ditty", Goss "twittering notes", Hatch "inexpressible" and Allen "like someone climbing over a wire fence".

The song is indeed hard to put into words though it is far from "inexpressible". Before giving the actual song however, the method of delivery should first be outlined.

Most of the singing, by far, is done from a clod or sign-post stage (the greatest height being a sample apartment on the area at Evanston), and breeding areas were rarely without a Lark in this performance. This was especially true after sundown, as Seton describes, but the first morning notes were delivered from the air contrary to his observation that they are from the ground. These surface songs are merely repetitions of the flight deliveries yet frequently they are not so full nor so complete.

The urge to the flight song came frequently after the male had succeeded in eliminating an intruding Lark from his territory and almost invariably, during the period of incubation, the male would go into flight song upon the approach of a human intruder. Or, if not at the first approach, he could be forced to do so by driving him about his territory for a time. He begins the ascent by a deliberate climb, step by step, by flutters and pauses, to his stage in the sky. This climb is deliberate, purposeful, its meaning cannot be misconstrued, though the bird makes no sound, as a rule, as he ascends. When satisfied with the altitude, he opens wide both wings and tail and as he sails he sings, at first deliberately, then faster and faster until the ending is a jumble of trills. The song may be written as, "pit-wit, pit-wit, pittle wittle, little, little, leeee".

Each song is two seconds or less in duration and between each the Lark ascends with from three to four flutters of four wing-beats with a pause of one or two beats of time between each, before spreading out for the next delivery. The actual singing occupies less of the Lark's time than the efforts of the bird to maintain the altitude, but this is more than compensated for by the many minutes the Lark remains in the air. One or two record flights lasted more than five minutes.

If appearances do not deceive, the Lark just maintains his altitude after the singing begins and neither appreciably rises nor sinks thereafter until the finish, in the majority of cases.

The finish of the flight song is the most spectacular event of all. When the song is ended the bird suddenly closes his wings,

turns headward to earth and drops, drops, drops for four, five or six seconds in certainly the most thrilling dive ever indulged in by living creature. The bird, when within twenty or thirty feet of the earth, opens his wings and alights at his starting place or, if it be at a distance, starts off nonchalantly to seek it as if it were a mere commonplace to pitch several hundred feet from out the sky.

This type of song I have named the "intermittent" and the above description is its most frequent and typical rendition. It is subject however, to many modifications. Once or twice the Lark started to sing shortly after leaving the ground and continued to sing, at intervals, on the upward climb. A few times the Larks failed to maintain their altitude and dropped lower and lower until the final dive was very short in duration. Still, it may be noted here, no Lark ever finished a flight song without the dive however near the earth it might be. This dive is reserved as a climax to the song and it seems as necessary a requisite as the notes themselves.

A rarer type of song than the "intermittent" is now and then delivered in the air. To it I have given the name "recitative", for the Lark, during its rendition, then beats the air steadily with wide, slow strokes (apparently much like the Skylark in song), and delivers the while a vigorous, even discourse of notes. This song is a steady "pit-wit, wee-pit, pit-wee, wee-pit". This "recitative" is frequently the prelude of the "intermittent" in flight song, lasting however but a very few seconds; and, occasionally, it is given at periods other than the beginning, but it never occupies so much of the time as the "intermittent".

If the wind is calm the bird describes large rough circles overhead; if the wind is violent the bird heads into it throughout. The climb upward is at a considerable angle and may be fairly direct or describe uneven spirals. Most frequently the bird drops straight downward, now and then at an angle, as if slipping down a steeply inclined roof, but nine times out of ten he drops directly onto a favorite song post which he must have been able to see at the elevation from which the drop was begun.

I have never seen a female Lark show the slightest indication that she was aware of a male in flight song but I have seen males on the ground cock their heads sidewise, fully aware, of that other bird overhead. But it is probable that the purpose of the

song is to inform the other male of preempted territory and female ears are of little concern to the chorister.

One thing of more than unusual interest was noted in respect to the frequency of flight songs, viz., that never were two birds in the air at the same time. No matter how many males were in the vicinity the one in flight song had exclusive privileges over a wide territory, undisputed, though another might go up as soon as the one in flight came down. Flight song territory is thus much larger than the surface territory; territory boundaries are not vertical for any great height.

As has been noted, singing from the ground was a fairly consistent performance through the day though perhaps a bit more frequent in the late afternoon. This day-time song from the ground was usually the "intermittent" type. But after sundown, in June at least, the Larks had a vesper service which was almost exclusively "recitative". At that time, as the stars came on, they sang "pit-wit, wee-pit, pit-wee, wee-pit" on and on, minute after minute, pausing only now and then for breath or a moment's intermission by singing "pittle, wittle, little lee".

Quantitative studies of song.—The height at which the flight song is delivered has been a matter of considerable speculation by several writers. Thus Eaton (1912) says "reaching a height of several hundred feet", Townsend (1920) "sometimes out of sight in the low-flying clouds", Merrill (1888), in describing the song of *O. a. strigata*, writes that, "The height at which they fly is so great that often they may be seen to poise and then to resume their circling flight before any sound reaches the observer." This last estimation making the height between one-thousand and two-thousand feet, for the "intermittent" song or length of time of sail in *praticola* is just short of two seconds. Sound travels 1090 feet per second. This is, of course, an impossibility for at 1000 feet the Lark is invisible even to eight-power binoculars. Patch, Bailey and others mention that they fly out of sight.

I attempted to secure an accurate measure of the height at which the song was delivered in order to settle the matter definitely. Three methods were employed: (1) by timing the drop with a stop-watch, (2) by using a large quadrant to secure a triangulation, (3) by measuring the length of the bird in the air

with the aid of a scale in my binocular. Of these three the last gave the most nearly accurate and most extensive results.

The stop-watch method must take into consideration too many elements to be reliable. Thus, though the rate at which an object will fall in a vacuum is definite enough, the Lark is not in a vacuum. Furthermore it often has fallen considerably in altitude while singing before beginning the final drop and, frequently, it does not always fall directly down. However, a good many timings of the drop were made, the average of the whole being about five seconds. The bird thus, if in a vacuum, would have fallen, on the average, 496 feet. This, at least, gives an idea of the height but is greatly in error when air-friction and the lowering of altitude before the drop are considered.

With one person to sight along the movable arm of a large levelled quadrant to secure the angle of a Lark in the air (but not directly overhead) and another to get directly beneath the singing bird a triangulation could be secured. Thus, on one occasion, this angle to the bird in the air plus the horizontal distance away were obtained. This is a simple trigonometric problem in which two angles and an included side are known. The result was about 350 feet. However this method is faulty, not in technique, but in execution. In the first place, two people are necessary to execute it; secondly, it is difficult to get to coincide the obtained angle and the horizontal distance at the same time for the bird is constantly moving; lastly, a bird at maximum height cannot always be found with the unaided eye.

With the binocular scale and the known length of the bird (about 8 inches or 19.0 cm.) estimation of height becomes relatively simple and accurate. It is necessary merely to find the value of a unit of the scale for the length of the bird at a known distance. The value of the scale unit for an object of known length at any distance can then be calculated from this known basis. It is merely a simple task of calibration.

Thus, by using an old military binocular with an ocular scale, accurate measurements of the height of 25 song flights were obtained. The lowest noted was 270 feet, the highest 810 feet. The majority were delivered at about 540 feet. The average, properly weighted, was 464.4 feet.

Visibility of the Lark in flight song.—The question of whether or not the Lark goes out of sight depends upon many

things: eyes, light, clouds, time of day. In morning or evening, on clear days, it was always possible to find or to follow the bird with the unaided eye for the light, low in east or west, then does not blind the eyes and aids by giving the bird a shadow on one side or the other. With the sun nearly overhead the bird goes out of sight quickly for the light blinds and the size of the bird is not accentuated by a side shadow. With clouds above, of any description, a singing Lark can always be found for then it is a moving silhouette nearly always sharply outlined against its background. Under any circumstances the singing bird was always visible to an eight-power binocular if it were followed as it ascended so that its position could be ascertained.

The songs, whose heights were obtained, were listed by months to see if the bird averaged higher or lower in one part of the season than in another. Nothing is evident, however, in the material at hand for, though the record height was in March, songs nearly as high occurred in June. Differences in heights then were matters of individual variation or the result of weather conditions.

Duration of the flight songs.—Thirty-two songs were timed with a watch from the beginning of the ascent to the final drop. One minute was the shortest of which there were four; five minutes was the longest of which there were five. The average for all is 2.34 minutes.

Number of songs per minute during the flight.—Since the "recitative" is a continuous jargon of notes its repetitions could not be timed. Its duration in a flight was rarely more than five seconds. The "intermittents", that is, the songs given while the bird is sailing, are repeated at remarkably regular intervals. The average number of these per minute, in an extensive series of counts, is 11.9.

Relation of the singing male to the incubating female.—Mouseley (1919) gives the distance from the nest at which the male Lark sings (when on the ground), at 32, 34 and 21 yards for three different nests. His figures are a bit too conservative, even for averages, for the Larks at Evanston or at Ithaca. By referring to Table 15 it will be noted that the male, in this case, preferred a song post at 50 yards, sang as far as 100 yards from the nest, averaged 38.66 yards. Ithaca birds,

with larger territories, sang even farther away, frequently at 150 yards.

Summary.—The song of the Prairie Horned Lark is, all in all, one of the most remarkable activities in the bird world. With a season from January to July, an optimum in May, a daily period from 4:00 A. M. to 8:00 P. M. (in June), a flight song with an average height near 500 feet, two types of delivery on the ground or in the air, and an evening's vesper that outlasts all others—it becomes an exhibition above challenge.

Fig. 1. The territory of a male Prairie Horned Lark, Feb. 7, 1926, at Evanston, Ill., as marked out by the song posts of that date.

Nesting Territories

Since the publication of Howard's (1920) now famous book on "Territory in Bird Life" no extensive study of a bird is complete without considering this important phase.

Evanston.—The earliest delimiting of territory at Evanston was noted February 7, 1926. A male bird, on that date, marked out the area as shown in Fig. 1. Only on one border did he come into contact with another male and there considerable fighting occurred. From a territory such as this a male bird will not leave no matter how consistently one annoys him by driving him from place to place. His usual relief is to go up into flight song. A female was noted with him from time to time though she did not persist in the territory. Several other birds on the same area, this date, had established song posts and territory boundaries.

There was no method of knowing, at Evanston, whether the same territory was retained throughout several nestings because of the large number of birds on the area and the consequent confusing of individuals. Each large snow storm would destroy song posts and disrupt territories and data are not at hand to show whether the former territories were returned to when conditions were favorable, though such is probably the case since it proved so at Ithaca. The chief single item in modifying territories, once they were established, was the growth of vegetation and this in June and July would narrow them down, pinch them up or cause their abandonment entirely.

At Ithaca I forced a male to mark his territory for the first time on March 13, though song posts had been established some time previously. This was territory "A" (see figure 2). Subsequently territories "B" and "C" were plotted as noted in figure 2. Of interest is the fact that the territory which the male marks when forcibly driven from song post to song post is somewhat smaller than that which he will delimit if allowed to go voluntarily from place to place. The reverse of this, one would think to be the case. Of course not all portions of the area are occupied with the same frequency, in fact the bird goes but rarely to the remote boundaries. Those regions in juxtaposition to the neighboring Lark are, as one might well suppose, the positions most frequented, for it is here that limits of the area must be most rigorously guarded.

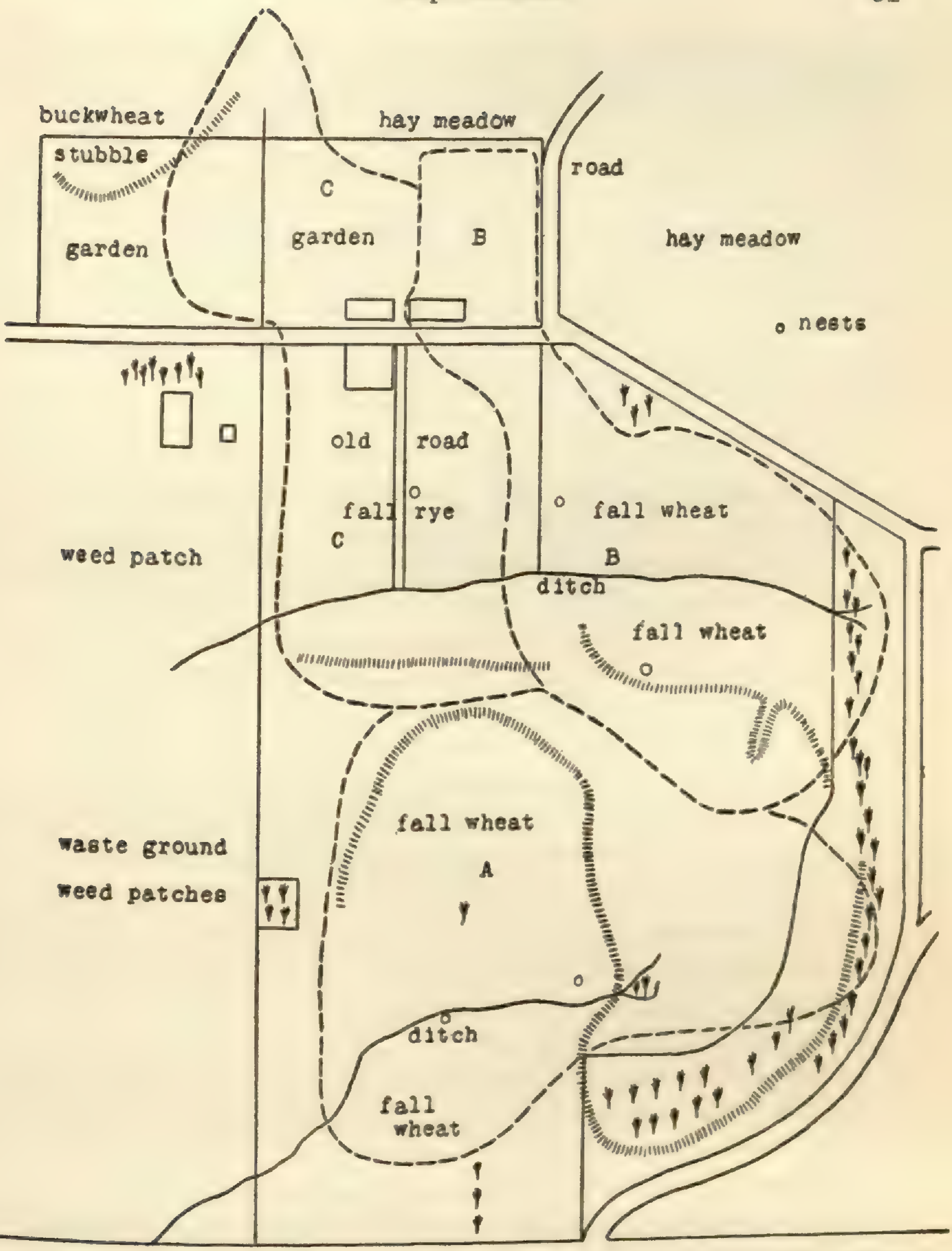

Fig. 2. The territories of Prairie Horned Larks A, B and C in March and April at Ithaca, New York.

Boundaries of territories seemed to be limited, in a general way, only by the size of the suitable area and by the number of males attempting to possess it. Thus, at Evanston, where the

number was higher, proportionately, than at Ithaca, the average territory was only about 100 yards in diameter whereas at Ithaca they extended out to lengths of 300 yards and breadths of 200 yards in some cases. The territory of pair "D", a short distance from "A", "B", and "C", was a field of plowing just six acres in area which pair "D" called their own exclusively.

But though some boundaries might be established by the margin of unsuitable territory there was a limit even where suitable ground still persisted. Thus the old stubble field, which was later plowed and sowed, extending off to the northwest from territory "C", was eminently suited for Larks yet the "C" male was never seen farther than the boundary noted in figure 2.

That invisible boundary, that the male birds put up between themselves where their territories coincided, was of the greatest interest. The boundary between "A" and "B", "C" and "A" was a ridge, extending into a fair hill on the east. It is not strange that a natural marker, such as this, should be used to delimit the area. But the line that was laid down between "B" and "C" was over a perfectly smooth stretch of ground with no natural indications of any kind. Yet these two birds recognized it within twenty or thirty feet for a length of more than 100 yards. And here they posted themselves for the greater amount of time, to see that the other respected that invisible, but to them, quite definite boundary.

History of territories in subsequent nestings.—The observations at Ithaca followed Larks "A", "B" and "C" throughout the season from March to late June and through a number of nestings (see Tables 4, 6, 8, 9, 12, 13, 24, etc.). It is apparent that, except for one influence, the territories would have remained unmodified from first to last. That modifying influence was vegetation, here tall wheat. Thus territory "A", entirely within the fall wheat, was completely abandoned at the close of the second nesting in May. Territory "B", partly on the garden and partly on the fall wheat, was reduced in May on the east in the fall wheat portion, to little strips running up and down from the ditch there which had been washed bare of seed in the fall rains (Fig. 3). These areas, in June, were finally no longer tenable and the "B" pair was forced to a territory on the garden less than 50 yards wide (see Fig. 4). The territory of "C" was shortened to the ditch on the south but otherwise remained

essentially unaltered. Now, if ever, should have come a change in the "B"-"C" boundary. "B" was reduced to straightened quarters; "C" still roamed over a region more than twice as wide. I noticed a little more fighting now than usual but, with the exception of a possible shift of a meager twenty yards or so that same invisible, almost invincible boundary, erected in the storms of March, still held, unaltered, almost unquestioned.

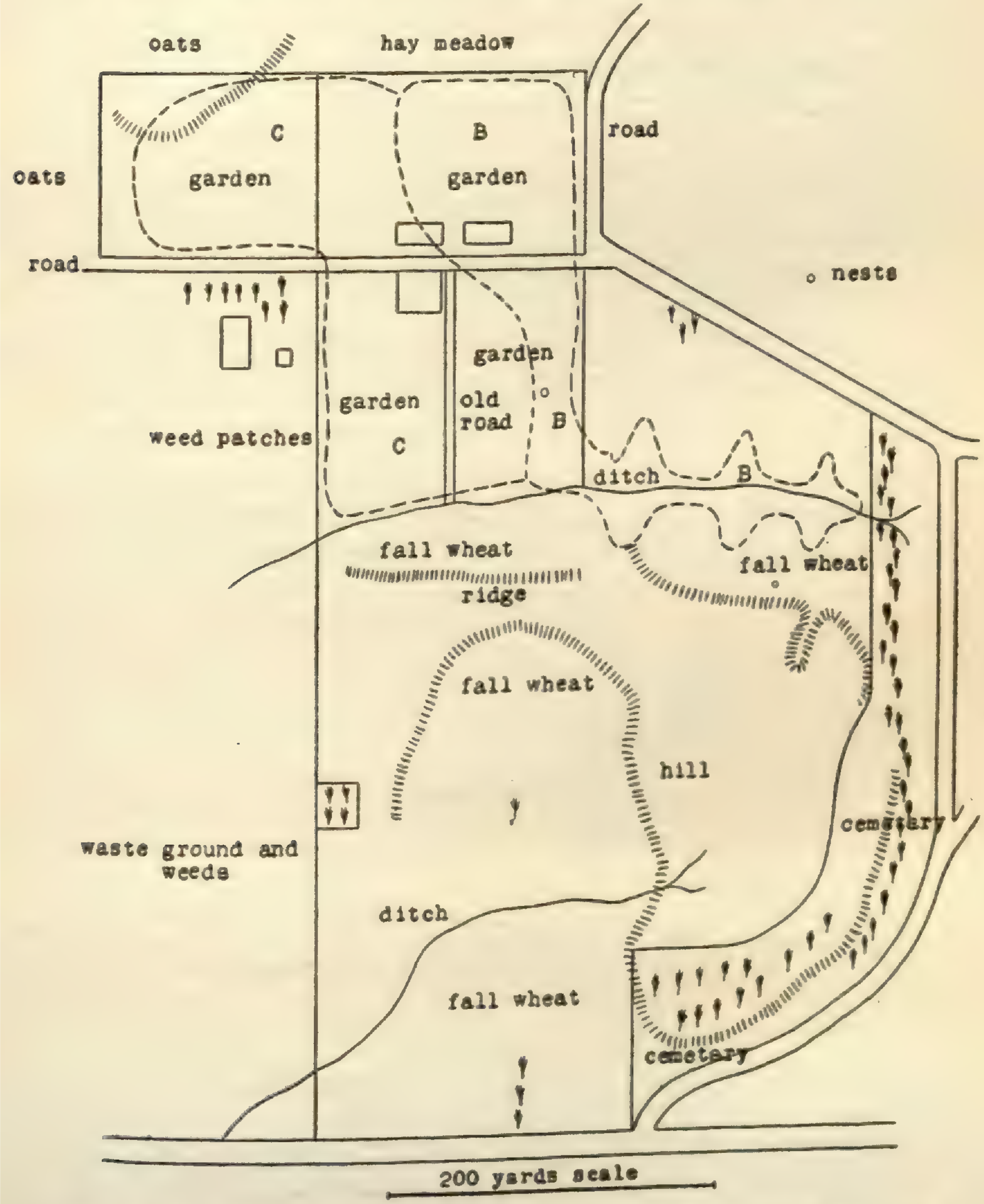

Fig. 3. The territories of Prairie Horned Larks B and C in late May at Ithaca, New York.

The south portions of the gardens had been in fall rye, but small areas of this were plowed under from time to time and thus exposed bare ground so that parts of this region were occupied throughout. The plant-stuff under cultivation, up to July, did not so cover the ground but that the gardens remained, until that time, quite suitable. (Incidentally, on the bare ground of this garden a flock of twenty to thirty Larks was seen Aug. 8, 1927.)

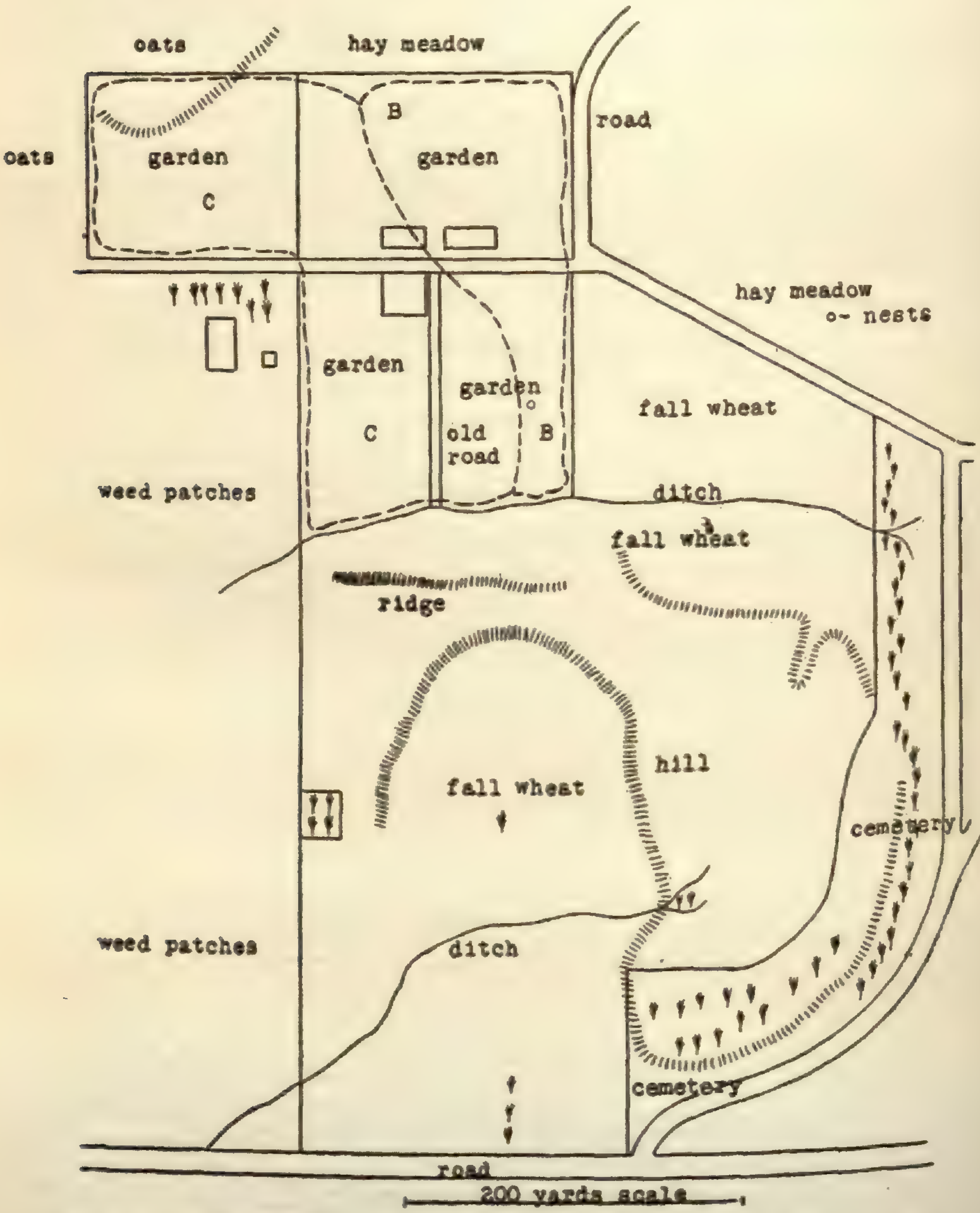

Fig. 4. The territories of Prairie Horned Larks B and C in June at Ithaca, New York.

Feeding in relation to nesting territories.—The males were on their areas so religiously that most of their feeding must have been done there too. However, now and then, one would be seen to fly up and out of sight as if intent on a considerable journey. These journeys at Ithaca were to the northeast and to the south. The attraction to the northeast was not ascertained but to the south was a stubble field with patches of *Setaria*. This was, apparently, a neutral feeding territory for several Larks. All observed feedings of the female were also within the territories at Ithaca, though at Evanston the female would go out considerable distances, clearly outside the nesting territory, though she gathered much food, as well, within the immediate vicinity of the nest. Incidentally, it should be noted, the female would mark out the territory if she were driven from place to place, though, being quiet and less obvious than the male, it was difficult to follow her for any length of time.

Nests were placed, of course, in these territories and placed with little regard to the center of the areas. "B1", for instance, was on the southeast margin whereas "B3" was on the extreme west. For complete data of nestings see Table 9. It is probably unnecessary to say that, though the male established the bounds of the territory, the female chose the nest site. Finally, it should be noted, that in one or two cases at least, the Larks were mated before territory bounds were definitely established though the reverse seemed true of others.

Summary of nesting territories.—Territories, at Ithaca and probably also at Evanston, were established very early in the spring and maintained with the same boundaries,* wherever possible, throughout the breeding season. Any change they were suffered to undergo came about with that one factor which the Prairie Horned Lark cannot endure, the advent of heavy vegetation.

Courtship

Song, the establishment of territory, battles at the boundaries, all these are part of courtship and have been discussed in preceding paragraphs. A few more items regarding fighting of

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* As will be noted later the fourth egg of female "B" was peculiar in that it had less pigment than the other three. Its occurrence in the second and third nests in the "B" territory in 1927 served to clinch the identity of the territory (though the birds all came to be known individually). In a letter received from M. D. Pirnie at Ithaca, dated April 12, 1928, he tells of a nest in this same territory with the same type of unusual egg.

males, and females, with a description of the strutting male will close this phase of reproduction.

Fighting.—As has been pointed out, territories are established very early in the season and after that time all fighting between males occurs along those boundaries of their territories which are in juxtaposition with those of a neighboring Lark. Fighting, prior to the establishment of territories, is promiscuous. All quarrelling takes place in the air. Never once did I see a battle on the ground, though Sutton (1927, p. 133) mentions "tussles on the ground". At the boundary dividing opposed territories the two males will most frequently be found. Here they remain together, seemingly most friendly and amiable except for an occasional sharp call note or a little strut with horns up, tails spread, wings adroop. Now and then they will approach each other in this attitude and peck away at the ground, furiously, like two cock roosters in an intermission of battle. But if, for any reason, one male attempts to fly, or if an intruder flushes both of them, then up they go, dash against each other, tumble over and over, an animated bundle of struggling feathers. Having indulged in wing to wing combat for a moment they finish off with a most curious game of tit for tat: one chases the other for a few feet in the air, invades thus the fleeing one's territory, the pursued promptly turns pursuer and in turn gets into his neighbor's territory, when the game is again reversed. So back and forth they go, one now chasing, next being chased and if the end of the game depended for its conclusion that neither should be upon the kingdom of the other then the ending would never be reached. Finally, however, one tires and goes off at a tangent while the apparent victor drops to a song post and there sings his song of triumph. But not for long, for soon the other is back at the boundary and friendly enemies they become again. For all this activity from March to June, so far as I can see, no harm is ever done.

Reactions of male and female Larks to each other.—The female is, at nearly all times, most curiously indifferent to the male. Only once did I see her flutter and crouch before him as one observes the female House Sparrow do so frequently. The female Lark thus has no courting maneuvers, though Sutton (1927) remarks a thing the writer has never observed in spite of intense observations, namely that the female answers the

male's full song "with a bright snatch of her own." The male, though, stays with her assiduously during the nest-building and egg-laying and may be observed frequently strutting with wings dropped, tail spread and horns up. Furthermore he has a little note of greeting that he reserves for her. It sounds like "check" or "cheek". On only one occasion did I see a female become pugnacious toward another Lark. In this instance she was guarding a youngster just from the nest. A neighboring male, in curiosity over this activity, invaded her territory to investigate, forthwith she got up and had at him with a fury well worthy of an Amazon. But, inconsistently, a moment later she fled before him as he made a second sally.

In connection with this study of territories and courtship I should like, in conclusion, to make a few comparisons between these observations and those of others. They show, most clearly, the whole change in attitude toward the activities of birds in courtship and nesting since the publication of Howard's (1920) famous studies of "Territories in Bird Life." Thus Jones (1892), in one of the most anthropomorphic descriptions encountered, says of the Larks that if a second suitor appears on the scene and the female shows "no preference" then the issue rests upon a battle which is short and decisive. She accepts the suitor of the previous year unless he has been killed (Jones does not say how he knew this) otherwise two young fellows vie with each other. The female usually shows a preference otherwise a battle follows. In any case battle is the "court of final appeal." If a female loses a mate she at once "seeks another and always finds him." And many more similar and untenable comments. Though, on the whole, the account of Harris (in Bendire, 1895) is the most extensive and thorough of any in the literature, some of his observations too are not now, with our present knowledge of the significance of territories, tenable. He says, for instance, after giving an admirable account of the manner in which Larks fight, when "suitors for the same female": "The victorious suitor then quickly returns to his coveted mate and struts before her with raised ear tufts and trailing wings, very much in the same manner as the English Sparrow." Lastly, and scarcely justifiable in the light of modern research, Sutton (1927) writes, "I believe the birds are essentially pacific and that males, rather than have a prolonged

fight over a certain female, give a chosen one and search in to elsewhere for a mate.'' But it is evident now that the fighting is not for a female but for the defense of a boundary, that fighting may be most vigorous before a female arrives or after she is incubating and that, in the case of the Lark, very little or no fighting occurs during courtship, nest-building or egg-laying for then the male stays within the bounds of an established territory and most sedulously attends his mate.

The Nesting

Season of nesting.—One would expect the dates of nests and the dates of song to correspond, and so they do, roughly. Song begins in late January, nests, as a rule, in March; song ceases in early July but nesting may not cease until August approaches.

The beginning of songs in January, in the depth of winter, in a setting of barren, wind-swept, unprotected plains and hills is not more incongruous than an incubating Lark sitting on her eggs in the sleet and snow of March squalls.

Four records of February nests have been found in the literature: The first of these is that of Linden (Forest and Stream XIV, 489) who found ''*Eremophila cornuta*'' with half fledged young the middle of February at Buffalo, New York. This article has not been available to the writer and is given here on the authority of the statement in the Bulletin of the Nuttall Ornithological Club, 5, 1881, 50. The second is that of Nelson (no date but *circa* 1880), who, writing of birds of northeastern Illinois says ''Sometimes the last of February.'' The third is of a nest with eggs in February at Plymouth, Michigan, found by Mr. J. B. Purdy and reported by Cook (1893). The fourth February nest is mentioned in Bendire (1895), who writes of a nest ''found in the vicinity of Milwaukee, Wisconsin, Feburary 23.'' It is quite possible that February nests are not uncommon for the birds frequently in February, in my own observations, presented all the activities of nesting. Sutton (1917), Jones (1910), Barnes (1890) are a few among the many writers who mention the ''late winter'' or February mating activities of this Lark. Yet nests, prior to the beginning of incubation, are next to impossible to find, as will be shown later,

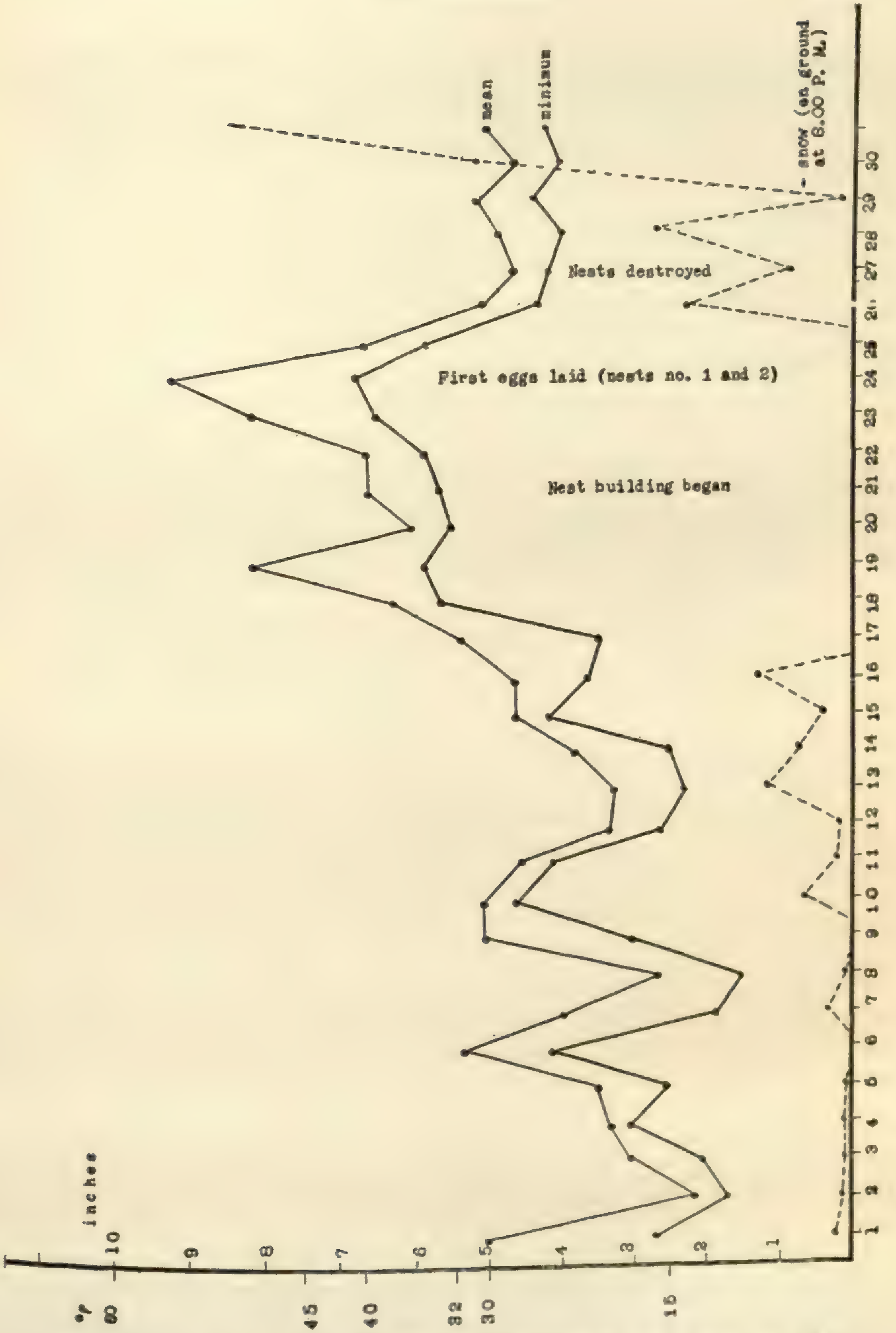

Fig. 5. Mean and minimum daily temperatures and snow on the ground at 7:00 P. M., for March, 1926, at Evanston, Ill., with a tabulation of the breeding activities of the Prairie Horned Lark during the month.

and it would be rare for periods of mildness in February to be sufficiently extensive to allow nesting to proceed to the point of incubation. Still it is probable that February nestings are not numerous for the ovaries of two females, one of which was mated, collected March 11 at Ithaca, were still several days from a period of maturing eggs, though the testes of males, collected the same date, were exceptionally large. But if February nests are the exception March nests are the rule from Kansas to Manitoba, from Manitoba to the Atlantic.

The following is an incomplete summary of March nestings by States: Kansas City, Missouri, March 12 (Harris, 1922); eastern Nebraska, late March (Bruner, Wolcott, Swenk, 1904); Marathon, Iowa, March 29 (Crone 1889); Manitoba, middle of March (Criddle, 1917); Quincy, Illinois, March 28, three nests (Poling, 1889); Champaign County, Illinois, March 15, March 31 (Hess, 1910); Michigan, before middle of March (Barrows, 1912); Ohio, last week of March (Jones, 1910); Ontario, March 28 (Eifrig 1911); New York, young able to fly April 7, 1878 (Langille, 1892); New York, late March (Bendire, 1895); New York, well started in incubation March 11 (Eaton, 1914); Pennsylvania, average March 25, earliest March 18 (Harlow 1918).

Before taking up the discussion of such a remarkable phenomenon as a Passerine nest in March, the few references before me pertaining to the last nests of the season will be given: Nebraska, "well into July" (Bruner, Wolcott and Swenk, 1904); Manitoba, July 14, eggs, "males still singing everywhere" (Criddle, 1920); Illinois, July 6 (Hess, 1910); Michigan, June 19 (Barrows, 1912). At Evanston, Illinois, the earliest nests were started, apparently, about March 21 in 1926, the last nest was destroyed by an unknown external cause July 12. If it had been successful it would have persisted to about July 20. Nest building began at Ithaca about March 11 in 1927, the last nesting would have persisted to June 28 had it not been disrupted by experimentation.

Explanations of March nests.—To show why a bird nests when it does has been the endeavor of many an ornithologist theoretically inclined. Food, necessities of the nesting site, physiology cycle, distance of migration, have all been advanced to explain the season of nesting of various species. No final

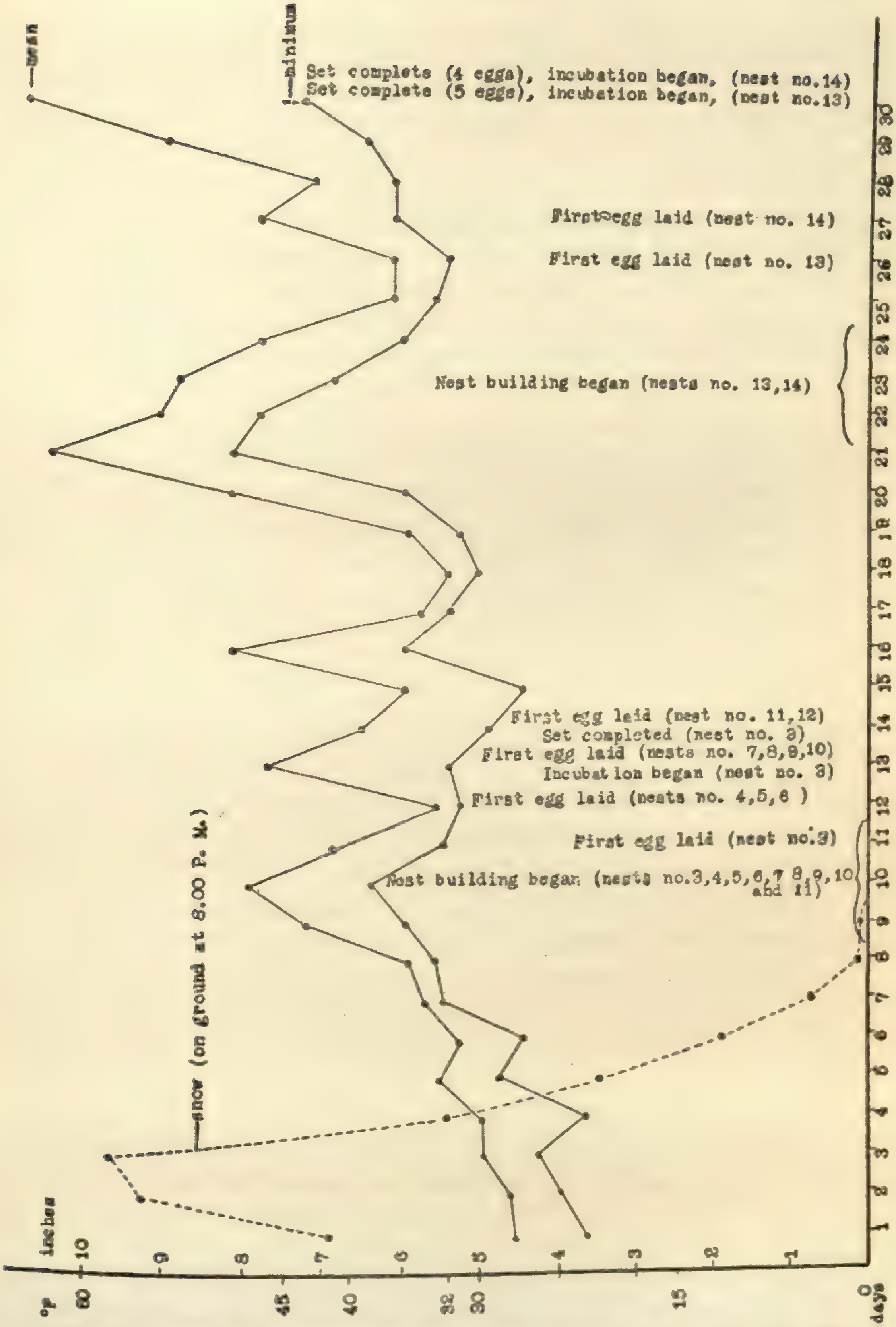

Fig. 6. Mean and minimum daily temperatures and snow on the ground at 7:00 P. M., for April, 1926, at Evanston, Ill., with a tabulation of the breeding activities of the Prairie Horned Lark during the month.

word has been said in any given case. This problem still remains one of the greatest, most fascinating enigmas of ornithology. Nor is there an adequate explanation for a March nest in the case of *Otocoris alpestris praticola*. If the bird nested in March only then the case would be clear for the argument that the barren nesting site is required—but it finds barrens into July; if it were true that greater food opportunity existed in March and not in other months there would be a good cause for nests at that season—but many young die of starvation even in April (see tables 22,23); the argument that the season is early because the bird arrives early is good but so does the Goldfinch and the Waxwing, and they delay to late June or early July before starting; the physiological cycle is at the bottom of it but why such a cycle? Why nestings that are snowed under in March when the season extends to July?

Before going further with an attempt to explain this phenomenon I wish to present a study of the possibilities of success of March nests in two localities of their range. By a strange coincidence the March nests at both Illinois in 1926, and at Ithaca in 1927, were destroyed by a heavy snow late in that month and early in April. From these two observations I was led to believe that the majority of March nests, at these latitudes, would be unsuccessful. To prove or disprove this I obtained weather summaries running back to 1910 for the Chicago region, and to 1916 for the Ithaca region.

Weather control of March and April nests.—First, however, by a study of known March and April nestings, it was possible to learn the temperature and duration of that temperature that was required before a nest would be started. This led to a very remarkable discovery (see Figures 5, 6, 7, 8) namely, that the initiatory temperatures was a mean somewhere between 40 and 45 degrees Fahrenheit and that with one exception it extended over a period of more than two days. The exception was an April nesting which was begun the first day the mean was above 40 degrees F., but even here two birds, one of which was known to have nested in March, did not begin their renesting until the second warm peak when the mean was again above 40 degrees F. and for several days in succession. Knowing, thus, what conditions are necessary to initiate a March nest, it next became necessary to consider what conditions will destroy it.

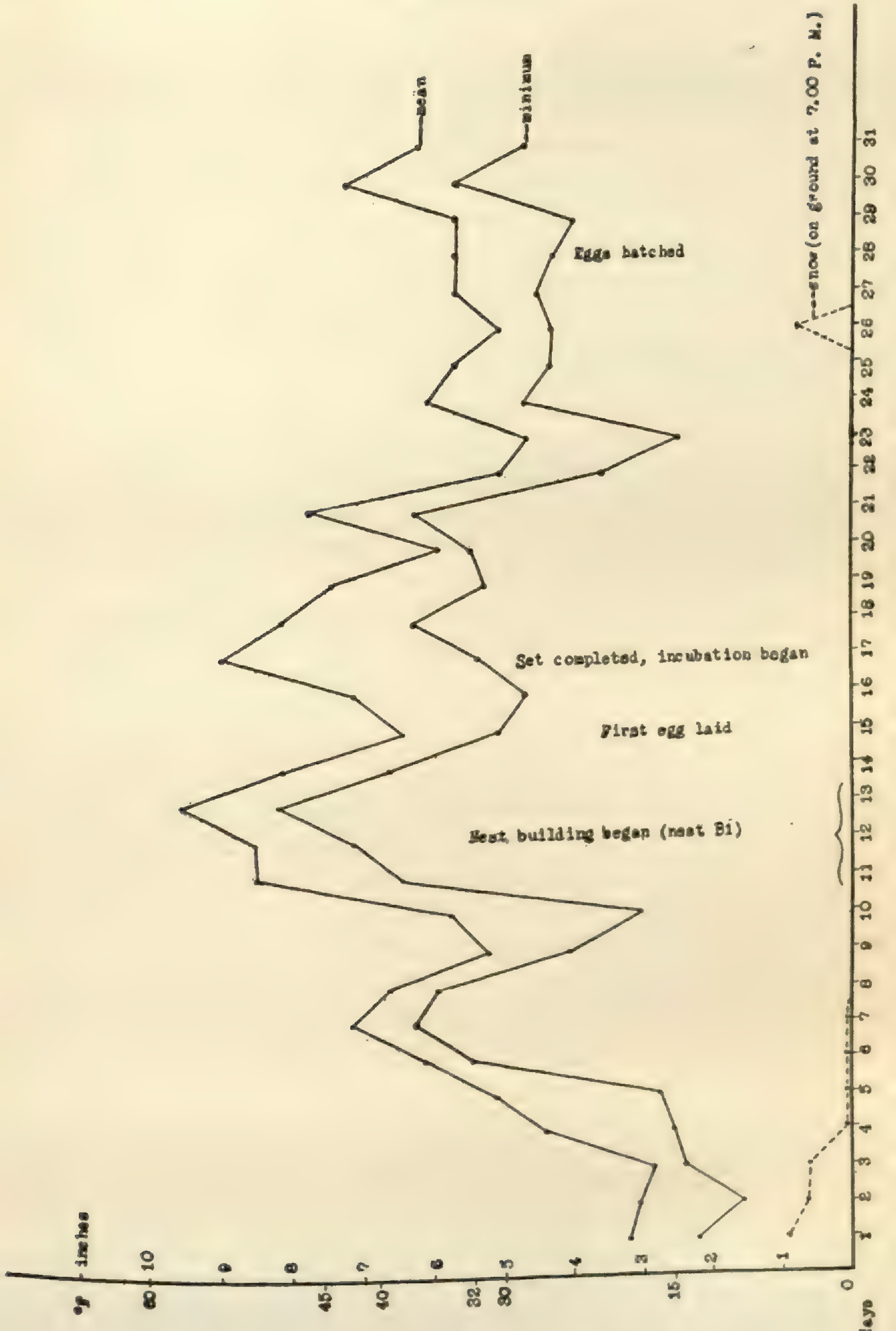

Fig. 7. Mean and minimum daily temperatures for March, 1927, at Ithaca, New York, with a tabulation of breeding activities of the Prairie Horned Lark during the month.

It is probable that, once a nest is started, subsequent cold weather will not inhibit it—the physiological processses are not checked. To substantiate this observe the weather of March, 1927, that intervened between the initiation of the nest about March 11 and its ultimate destruction at the end, or, again note that the nest begun April 6, 1927 (Fig. 8) passed through several nights with temperatures much below freezing immediately thereafter but the clutch was completed in record time (indeed the eggs must have survived this cold uncovered). If, then, cold weather alone will not destroy March nests their meteorological enemy is restricted to snow. Without a doubt the female bird will incubate through a slight snow without relinquishing her eggs. Note that a slight snow fell March 26 (Fig. 7, also Plate VII, Figures 2), but the nests were not abandoned because of this. Many writers have found Lark nests in the snow and Langille goes so far as to say that a Horned Lark flushed out from under "three or four inches" of snow, April 6, 1880 (Langille, 1892), but it is probable that the bird would not have remained under the snow for more than a few hours. The snows of early April 1926 and 1927 destroyed all nests and there is no doubt that any snow of three inches or more that lasts two or three days will cause the destruction of nests. Bendire (1895) in quoting Harris, says: "The weather during the latter part of March (in western New York) is often very pleasant and warm, only to be followed by a heavy fall of snow about April 1, when a good many unfinished nests and incomplete sets of eggs are snowed under and deserted by the owners; in fact, only a few birds will cling to their nests under these circumstances, as I have found many abandoned ones in different seasons."

Now, having concluded that nests would be begun in March whenever two or more days of a mean temperature of 40-45 degrees F. occurred, and that they would be destroyed by a snow of three or more inches lasting two or more days, the success of hypothetical nesting at Chicago and Evanston could be tabulated from the weather summaries. The only record for snow on the ground in these summaries is at 8:00 P. M. at Ithaca or 7:00 P. M. at Chicago and this is exceedingly conservative as far as the total amount of snow is concerned. The result of this tabulation is shown in tables 1 and 2. The interest-

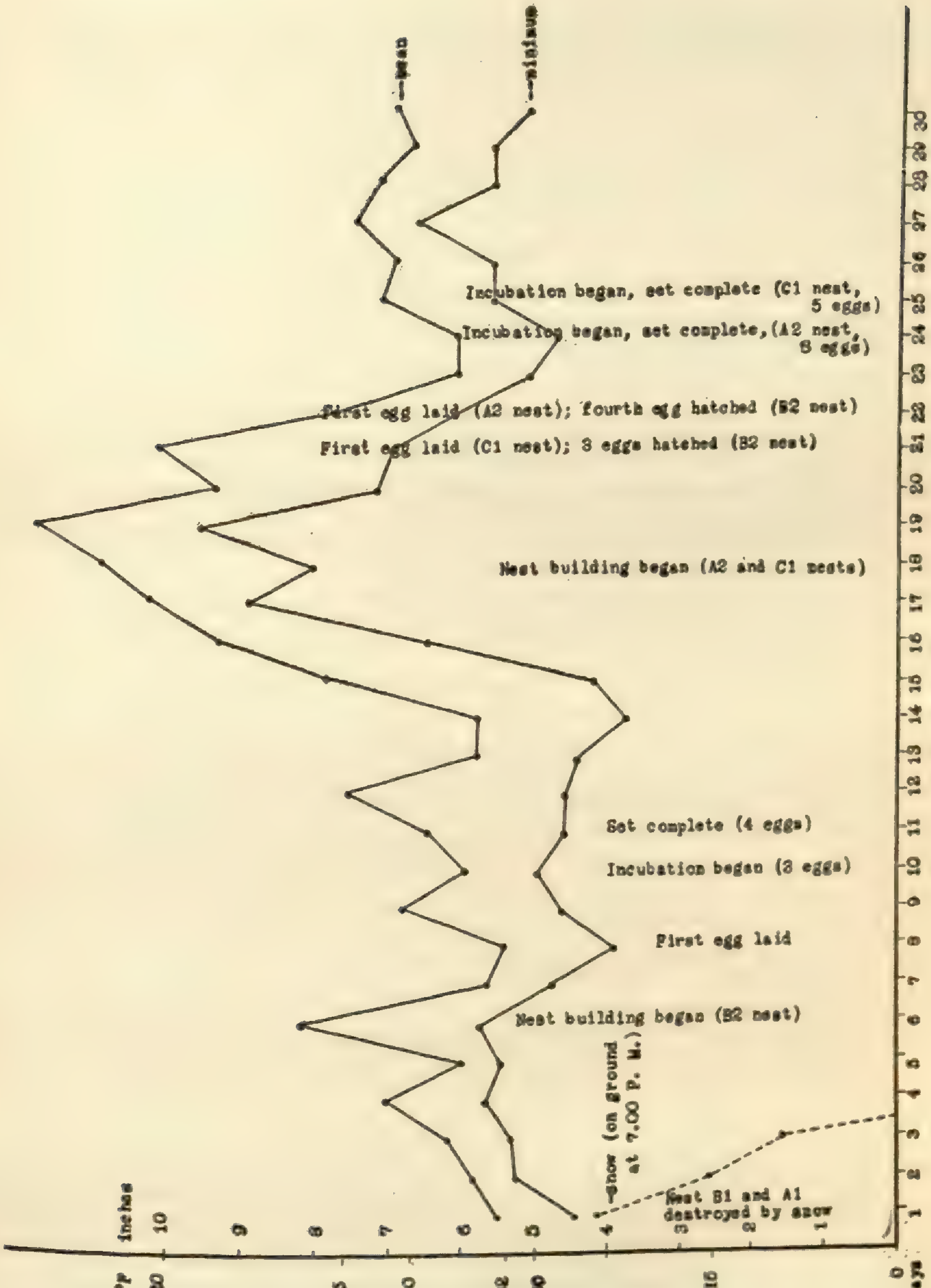

Fig. 8. Mean and minimum daily temperatures and snow on the ground at 8:00 P. M., for April, 1927, at Ithaca, New York, with a tabulation of breeding activities of the Prairie Horned Lark during the month.

ing thing to be noted is first, the surprisingly large number of opportunities for successful nesting there are in March and, secondly, the fact that nestings in northern Illinois have a greater chance than at Ithaca, New York.

But the reason for March nests remains still incompletely explained. The habit was probably acquired very early and

TABLE 1

Hypothetical March nestings of the Prairie Horned Lark with the probable ultimate success or failure with regard to snow, in the Chicago, Ill., region, for the years 1910-1927 (excepting 1924).

Year	Possible* Nesting Periods in March	Dates of Deep Snow on Ground Subsequent to Nesting	Maximum Amount of Snow on Ground at 7 P.M.	Result of March Nesting
1910	2 to 6, 11 to 13, 18 to 31	None		Successful
1911	8 to 12, 19 to 22 24 to 27	March 27 to April 2.	2 in. April 2	Successful?
1912	Snow on ground throughout month.			
1913	12 to 14, 18 to 20, 23 to 24, 29 to 31	March 21	2.2 in. March 21	Successful?
1914	14 to 16, 24 to 31	None		Successful
1915	13 to 14, 23 to 25	None		Successful
1916	12 to 13, 24 to 26, 29 to 31	March 22	2.6 in. March 22	Successful?
1917	10 to 11, 20 to 31	None		Successful
1918	4 to 5, 8 to 9, 11 to 12, 17 to 22, 29 to 31	None		Successful
1919	15 to 20, 24 to 30	None		Successful
1920	9 to 11, 14 to 16, 21 to 31	April 4 to 7	6.1 in. April 4	Failure
1921	1 to 2, 5 to 21, 24 to 27, 30 to 31	None		Successful
1922	5 to 6, 9 to 16, 27 to 28	March 31	1.1 in. March 31	Successful
1923	1 to 4, 21 to 22	March 18 to 19	1.3 in. March 19	Successful (nest of March 21-22 only)
1925	6 to 10, 16 to 31	None		Successful
1926	19 to 25	March 26 to April 6.	9.9 in. April 3	Failure
1927	8 to 19, 25 to 31	None		Successful

*Not less than two days with a mean temperature above 40 degrees F.

NOTE: All dates are inclusive.

Summary: Number of years considered: 17
Number of years in which March nests were possible: 16
Number of years of successful nesting: 10
Number of years of failures due to snow: 2
Number of years of problematical success: 4

it has been carried eastward and northward with the recent extension of range into regions where it is obviously a greater incongruity than in the earlier home. For even in northern Illinois March nests are far more successful than in south central New York and the discrepancy would be greater between eastern Kansas and Manitoba. The question, at this time, must rest here with the conclusion that the origin of March nestings is not fully known but may have been developed as species-

TABLE 2

Hypothetical March nestings of the Prairie Horned Lark with the probable ultimate success or failure with regard to snow, in the Ithaca, N. Y., region for the years 1916 to 1927.

Year	Possible* Nesting Periods in March	Dates of Deep Snow on Ground Subsequent to Nesting	Maximum Amount of Snow on Ground at 8 P.M.	Result of March Nesting
1916	25 to 31	None.....	.....	Successful
1917	23 to 31	None.....	.....	Successful
1918	12 to 14 and 17 to 22	April 9 to 13.....	10 in. April 12.....	Failure
1919	17 to 18 and 25 to 26	March 27 to April 1.	5 in. March 28 to 29	Failure
1920	22 to 31	None.....	.....	Successful
1921	6 to 17, 20 to 21, 24 to 28	None.....	.....	Successful
1922	13 to 15	March 30 to 31.....	2 in. March 30....	Successful?
1923	21 to 23	None.....	.....	Successful
1924	28 to 30	April 1 to 3.....	7 in. April 2.....	Failure
1925	8 to 11, 17 to 19, 24 to 27	March 28 to 29.....	2.5 in. March 29...	Successful?
1926	None	Mean daily tempera ture below 40 degree s F. and snow on the ground throug hout month.		
1927	11 to 14, 18 to 19	April 1 to 3.....	4 in. April 1.....	Failure

*Not less than two days with a mean temperature above 40 degrees F.

NOTE: All dates are inclusive.

Summary: Number of years considered: 12
Number of years in which March nests were possible: 11
Number of years of successful nestings: 5
Number of years of failures due to snow: 4
Number of years of problematical success: 2

necessity in some earlier home where such nests were sufficiently successful to have been maintained; and now such nestings have been carried to regions where they may, eventually, be eliminated through natural selection.

Finally, before leaving this fascinating subject, it should be noted that *praticola* seems to be unique among all the Horned

Lark subspecies in this habit of early nesting. I have found no evidence, in the literature, that even such southern forms as *giraudi* or *chrysolaema* nest in March and *alpestris* does not begin until June in Labrador. Lastly Criddle (1917) notes that *enthymia* breeding in the same region with *praticola* at Aweme, Manitoba, does not begin to nest before May, whereas *praticola*, there as elsewhere, nests in March. The mystery of March nests, then, begins and ends in the Prairie Horned Lark.*

On finding nests and the reactions of nest-building and egg-laying Larks.—The first preliminary to the location of a nest is to find the singing male. Having done that one has an idea, within a hundred yards, perhaps more, perhaps less, where the nest is or where it will be located. But the nest is still far from being found. Mouseley (1919) writes that he locates the favorite song post of the male, then marks out an area twenty to thirty yards in each direction, this he examines carefully or watches the male until he flies to the nest. By this means he located three or four nests, one of which had young. Rarely, in observing the actions of Larks in thirty-one nestings, have I seen the male approach an incubating female unless the female was *first* disturbed. Likewise the "favorite" song posts of a male may be numerous and some as far as one-hundred to one-hundred and fifty yards from the nest. If there are young in the nest the male, in feeding, will, at times, give the location away more quickly than the female, in other cases the reverse is true. But, outside of a general indication of a breeding area denoted by song, the male has never been of great service to me in finding nests with eggs.

It is my belief that, except for mere accident and the rarest kind of accident at that, a nest cannot be found between the beginning of egg-laying and incubation. As far as I can ascertain from the literature, very few such have been found (excepting possibly McDonald, 1916) and, considering the unbelievable inconspicuousness of a nest even in the bare areas where it is placed, its chances of being found, unassisted by actions of the parent bird, are negligible. Neither female nor male approach a nest in this state and though one can know from the actions of the birds (extreme nonchalance, an infinity of leisure

* Since the above was written the writer has had the pleasure of finding, with a companion, Mr. Paul Walker, a March nest of *Otocoris alpestris actia* at San Jose, California (March 25, 1928).

for instance), the exact condition of their nest, to find it is another matter. Despite this fact and the knowledge of the hopelessness of such a search, I have gone over promising sites examining every inch for hour after hour until the sum total so spent had accumulated into days of time and have never found such a nest, i. e. with eggs just prior to incubation. Accidentally, however, students of mine located two March nests with eggs that had been abandoned as the result of early April snows.

It is easier, though by no means simple, to find a nest in the process of construction. The female at this time is assiduously attended by the male, and, in addition, displays a restlessness (runs back and forth, is quiet for short intervals only, flies up and away but shortly returns), quite different from any other period of the nesting. But she approaches the scene of her prospective nest with extreme reluctance while an observer is near, even within fifty yards, and hours of watching may be necessary before the nest site is located. Four recently excavated nest cavities were found by this method and one or two partially constructed nests. It should be added, however, that, though in one case material was added after the cavity was found, in no case was any nest completed after its discovery. Either the bird is so timid that she deserts these early starts upon the slightest interferences or so many starts are made (see below) that in no case have I been fortunate enough to find the one chosen for completion. Apparently Mouseley (1916), is the only ornithologist on record who has watched the evolution of a nest from the period of the excavation until the set was complete. And Mr. Wm. Chandler (Sutton, 1927) found a female building a nest that later had eggs, but neither of these gentlemen make clear just how they located the structures at their beginnings.

After the bird has begun to incubate the case is far different. Then, knowing that the female most frequently will leave her nest at from thirty to seventy-five yards, in advance of any intruder, in a very characteristic "casual-abandonment" flight low over the ground, one has but to march back and forth over the breeding territory until she is seen to leave. Frequently then it is necessary to reapproach the apparent nest-spot from different angles on subsequent visits before the nest is disclosed.

Some birds leave their nests at such a distance that they cannot be seen. However the male usually becomes attentive when the female is off and by watching him one becomes aware of her.

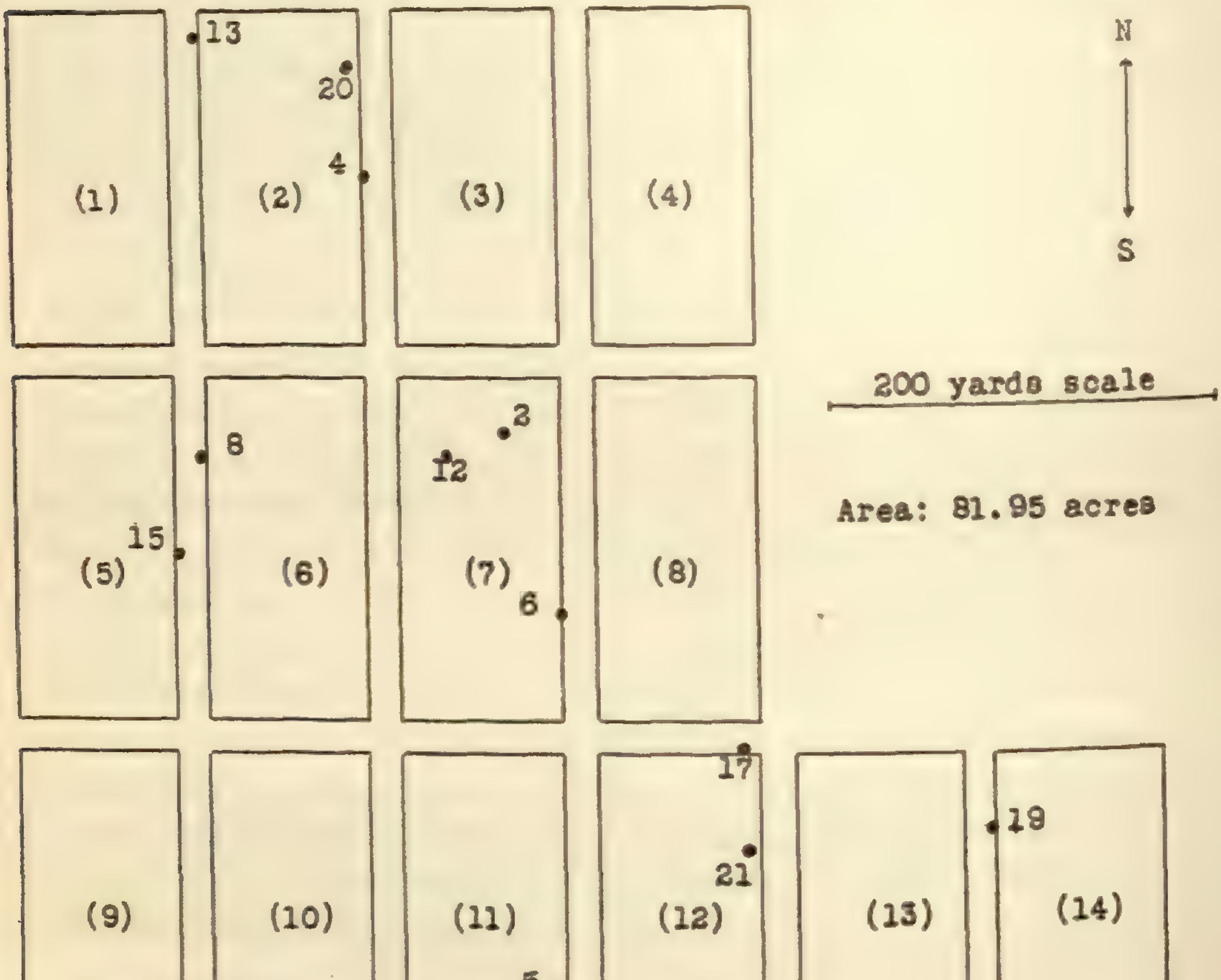

Fig. 9. Location of the nests of the Prairie Horned Lark on the Main real-estate Subdivision at Evanston, Ill., 1926.

Close attention then to the female may, after an uncomfortably long period, disclose the nest when she returns to it. If, for any reason, such as activities of farm horses, machinery, workmen, etc., near a nest, the female is kept for too long a time from it,

she will gradually lose her instinct of concealment by abandonment, show solicitude by her presence, by running here and there and in ground-picking, and finally go onto her nest with an observer comparatively close at hand. It should be added that, in a few cases, the female Lark may sit close and the nest then is found only by an accidental flushing of the incubating bird. Again as Harris (in Bendire, 1895) brought out, she sits closer toward evening and, as I have noted, when the day is very chilly. Sutton (1927) also, after a lengthy recital of the actions of a pair of Larks whose nest he was endeavoring to find and for which he describes many of the reactions tabulated above for nest-building and egg-laying birds (though these significances he did not realize), finally found his nest near dark by flushing a close-sitting female.

The remarkable luck of the writer in finding seven nests in one day (April 18, 1926) was because of some unusual circumstances. First, there were many Larks on the Main Subdivision at Evanston; secondly, all began incubation almost simultaneously (because conditions for renesting in April had suddenly become propitious, see Figure 6); thirdly, the most desirable nesting site was that of the grass strip between the sidewalk and the dirt mounds in the center of the street (see Plate XII, Fig. 1; Plate XIII, Fig. 2).

All that was necessary to find the nests here was to tramp these strips over and over until the nest of every bird that flushed was located. Since the day was cold and I attempted to approach against the concealing clump of verdure on the north side of the nest, many incubating birds did not flush until I was nearly upon them. To find their nests then, was simple.

Nests containing young shortly after hatching may be found by watching the female leave, as she does when incubating. Later the parent birds will give away the nests while carrying food. But, unless the position of the nest is spotted within a few feet, many minutes, sometimes hours, will be required even then to find it, so protectively colored are the young whether in down or juvenile plumage (Plate XXXIII, Figs. 1 and 2).

Nest Building.—The nest cavity seems to be dug by the female in all cases as no evidence of using a "natural depression" was ever noted in spite of many literature references to

TABLE 3

Locations and protections of nests of the Prairie Horned Lark at Evanston, Ill., 1926

Nest No.	Date Completed*	Environment		Protection	
		General	Immediate	Position	Character
1	March 22	Streetway	Dead *Agrostis palustris*	W.	Sidewalk
2	March 22	Old sand hazard	Bare ground, dead *Setaria*	W.	Dead stems of *Setaria*
3	April 11	Streetway	Dead *Agrostis palustris* and others	N. W.	Dead weed clump, sp.?
4	April 12	Streetway	Dead *Agropyron repens*, bare ground, *Taraxacum officinale*	N. W.	Dead *Agropyron repens*
5	April 12	Streetway	Bare ground, *Agropyron repens*	N. W.	Dead *Cirsium arvense*, dead *Agropyron repens*
6	April 12	Streetway	Dead *Agrostis palustris*	N.	Dead *Agrostis palustris*
7	April 13	Streetway	Dead *Agrostis palustris*, old boards	N.	Dead *Agrostis palustris*
8	April 13	Streetway	Bare ground, dead *Poa pratensis*	N.	Tuft of dead *Poa pratensis*
9	April 13	Streetway	New *Achillea millefolium*, bare ground, dead *Agrostis palustris*	W.	Tuft of A. *palustris*
10	April 13	Streetway	Dead *Agrostis palustris*	All sides	*A. palustris*
11	April 14	Within block	Bare ground, dead *Polygonum sp? Setaria*, etc	(None)	.....
12	April 14	Within block	Surrounded by dead *Poa pratensis*	N.	Tuft of dead *Poa pratensis*
13	April 26	Streetway	Bare ground, new *Agropyron repens*	(None)	.....
14	April 27	Streetway	Dead and new *Agrostis palustris*	N.	Tuft of dead *Agrostis palustris*
15	May 3	Streetway	Stems of *Oenothera biennis*, bare ground, dead and new *Agrostis palustris*	N. W.	Tuft of dead *Agrostis palustris*
16	May 7	Streetway	Bare ground, a little dead *Agrostris palustris*, dead *Cirsium arvense*	N.	Dead *Agrostis palustris*
17	May 9	Streetway	New *Agrostis palustris*, *Poa pratensis*, *Agropyron repens*	W.	Short tuft of *Agropyron repens*
18	May 21	Within block	New and old *Agrostis palustris*	N.	New A. *palustris*
19	May 22	Streetway	Bare ground, new *Hordeum jubatum*	N. W.	Tuft new *Hordeum jubatum*
20	May 25	Old hazard	Very short, new *Agrostis palustris*	N.	*A. palustris*
21	June 9	Old hazard	Bare ground, young *Ambrosia artemisiaefolia*	N.	*Ambrosia artemisiaefolia*
22	June 17	Old truck garden	Bare ground, *Brassica arvensis*	W. N. W.	New plants *Brassica arvensis*
23	June 22	Old truck garden	Bare ground, *Chenopodium album*	N. W.	*Chonopodium album* plant
24	June 27	Old truck garden	Young plants *Xanthium canadense*	All sides	*Xanthium canadense*

*Estimated.

the contrary. This cavity is most probably dug with the bill, though there is no positive evidence on that score. However Sutton (1927) after saying (page 136) that a "natural depression is sought," adds (page 138) that the "female was working busily . . . the bird dug at the earth with her bill and kicked the loose material out with her feet." Usually the excavation is made partly under a clod or a tuft of grass (Plate V, Fig. 2; Plate VI; Plate VII, Fig. 1). The bulk of the material placed in this cavity consists of grass stems and leaves and often heavier weed material with comparatively coarse roots and much dirt. The lining is usually of finer material, plant down, paper, feathers, fine rootlets. For a careful and extensive tabulation of nests, nest sizes, sites and materials see Tables 3, 4, 7 and 8. The photographs of numerous nests among the plates will give also the structure and location of nests at various seasons.

The time required for nest building was not ascertained definitely. Mouseley (1916) gives four days for this phase in a case he carefully watched after removing the eggs of a previous set. The eggs were taken April 14, the new nest was begun the next day, completed April 18, the first egg was laid April 9. My observations showed, in the case of renestings in April after snow had destroyed previous nests and in one case where cultivation destroyed a nest, that the Lark works at times considerably faster than this. Thus on April 6, 1927, at Ithaca, one Lark dug three cavities, almost completed the lining of one on that date (eight or ten hours), but then abandoned all of them. The nest she finally occupied was not discovered until after incubation had begun, but counting back from the hatching date, allowing the optimum incubation period (11 days), she must have completed this fourth nest-start between the 6th and the 8th, for the first egg was deposited on the latter date. It is probable that this nest was also begun on the 6th (for the female was repeatedly observed in the vicinity where the nest was finally found), and that she completed it in two days time or less.

Seasonal Variation in nest structure.—An often repeated statement regarding Lark nests must be considered before the subject is dismissed. Thus Davie (1889), quoting Jones (1892), Bendire (1895), quoting Harris, Hess (1910), Sutton (1927) as well as other writers, say that later nests are more poorly built than early nests. This is attributed to a lessened "necessity"

TABLE 4

Location and protections of nests of the Prairie Horned Lark at Ithaca, New York, 1927

Nest No.	Date Completed*	Environment		Protection	
		General	Immediate	Position	Character
B_1	March 15.....	Hillside, fall wheat...	Bare ground, rows of short fall wheat.....	W.	Short fall wheat
A_1	March 20.....	Fall wheat.....	Bare ground, row of short fall wheat.....	W.	Short fall wheat
B_2	April 8.....	Fall wheat.....	Bare ground, row of fall wheat.....	W.	Fall wheat
D	April 8.....	Plowed meadow.....	Scant tufts overturned timothy (*Phleum pratense*) bare furrows.....	N. W.	Tuft of dead, overturned timothy
C_1	April 21.....	Fall rye.....	Bare ground, rows of fall rye.....	S. E.	Heavy weed roots
A_2	April 22.....	Fall wheat.....	Bare ground, rows of fall wheat, young timothy.....	N.	Fall wheat
B_3	June 4.....	Bare garden soil.....	Bare, fine soil, 2 or 3 stems of rye.....	N. W.	Two small clods

*Estimated.

TABLE 5

The "pavings" of the nests of the Prairie Horned Lark at Evanston, Ill., 1926

Nest No.	Date* Completed	Position of "Paving"	Nature of "Paving"	No. of Items	Size of Smallest Item	Size of Largest Item	Miscellaneous
1	March 22	S. E.	Clods	Items run	together by rain		
2	March 22	E.	Clods	Items run	together by rain		
3	April 11	S. E.	Clods				Total dimensions 10.2 by 30.6 centimeter
4	April 12	S. E.	Clods	Items run	together by rain		
5	April 12	S.	Clods	50		1.8 by 2.9	Total dimensions 6.4 by 25.0 centimeters
6	April 12	S. E.	Clods	25	.6 by .6	1.2 by 1.8	Total dimensions 15.2 by 7.6 centimeters
7	April 13	S. W.	Clods	18	.6 by .6	1.2 by 1.8	Total dimensions 3.8 by 12.5 centimeters
8	April 13	S.	Clods	30	.3 by .3	2.1 by 2.1	Total dimensions 6.4 by 15.2 centimeters
9	April 13	S. E.	Clods	18	.6 by .6	2.5 by 3.2	Total dimensions 7.6 by 15.2 centimeters
10	April 13	All sides	Clods	15	.6 by .6	1.2 by 3.2	Scattered about nest
11	April 14						No apparent "paving"
12	April 14	S.	Clods	8	.6 by .6	1.2 by 1.8	Total dimensions 6.4 by 12.5 centimeters
13	April 26	N. E.	Clods	Items run	together by rain		Total dimensions 7.6 by 10.2 centimeters
14	April 27	S.	Clods	1			
15	May 3	S. E.	Clods	30		1.2 by 2.9	Total dimensions 9.6 by 12.5 centimeters
16	May 7						No apparent "paving"
17	May 9	S. E.	Clods	Items run	together by rain		Extended from nest 20.4 centimeters
18	May 21	S.	Clods	2			Very meager "paving"
19	May 22	S. E.	Clods	Items run	together by rain		
20	May 25	S.	Clods	Items run	together by rain		
21	June 9	S. E.	Clods	Items run	together by rain		Total dimensions 7.6 by 10.2 centimeters
22	June 17	S. E.	Clods	Items run	together by rain		
23	June 22	N. E.	Clods	Items run	together by rain		
24	June 27	E.	Clods	Items run	together by rain		

*Estimated.
NOTE: All measurements in centimeters.

Reproduction

for good nests, since "the season is warmer." Jones (1892) takes it as a matter of course and writes that nests in February or March "would very naturally be more elaborate and warmer while those in July would be very slight." I hesitate to attribute any such prescience to the Larks. I thought by weighing the nests to prove or disprove this, but the weighings show nothing (see tables 7 and 8) for the dirtier material of later nests overbalances any lessened bulk of material. It is true, in general, and in some cases conspicuously so, that later nests have less bulk, less material than earlier, even for the same individual (see Table 8.) The explanation for this lies, I firmly believe, merely in the fact that there is far less desirable material later in the season than earlier, for vegetation has grown up to conceal and to make inaccessible the dead grasses, or rains of May and June have rotted them down. To confirm this take the case of nests B_1, B_2, B_3 (Table 8). B_1, in March, was bulky, well made, of fine rootlets and weed stems; B_2, in April, was a flimsy affair of dirty stems and leaves; but B_3, in June, was well made, about as bulky as B_1. The explanation is simple. Just prior to the construction of this third nest a field of fall rye was turned under. On this overturned ground B_3 was placed and great quantities of fresh, fine rootlets and dead leaves of the rye were near at hand. Sutton (1927, p. 136) also attributes variations in nest structure to variations in availability of material and adds that first nests are better because there is more time before the "onerous duties of brood-rearing have been assumed."

One thing more is to be mentioned concerning the nests of the Prairie Horned Lark. This seems to have more than a little of prescience in it. By a reference to Tables 3 and 4 it will be seen that nearly all nests were, in spite of their open location, placed beside some protecting object, usually a tuft of dead grass. There is something more than mere chance operating here, that of more than thirty nests nearly all should have this protection on the west or northwest.

"Pavings."—About a portion of the rim of the nests of *O. a. praticola*, usually on the side away from the protecting clod or grass clump, there was nearly always a definable layer of material (clods or pebbles), which the Lark had laid down during nest building. Peabody (1906) has, very appropriately,

TABLE 6

The "pavings" of the nests of the Prairie Horned Lark at Ithaca, New York, 1927

Nest No.	Date* Completed	Nature of "Paving"	Position of "Paving"	No. of Items	Size of Smallest Item	Size of Largest Item	Miscellaneous
B_1	March 15	Pebbles	N. E.	17	.6 by 1.3	1.9 by 2.5	Weight of largest pebble 2.4 grams
A_2	March 20	Pebbles	S. E.	4	.5 by 1.2	1.6 by 2.5	Very meager "paving"
B_2	April 8	Clods, pebbles	S.	.....	.....	.....	Very meager "paving"
D	April 8	Clods, pebbles	S.	17	1.2 by 1.8	1.8 by 3.2	Total dimensions 8.9 by 8.9 centimeters
C_1	April 21	.....	.....	.....	.....	.....	No apparent "paving"
A_3	April 22	.....	.....	.....	.....	.....	No apparent "paving"
B_3	June 4	.....	.....	.....	.....	.....	No apparent "paving"

*Estimated.
NOTE: All measurements in centimeters.

Reproduction

called this a "paving." The first instance of this sort of thing seems to have been cited by Silloway in "Birds of Fergus County, Montana." Peabody (1906), refers to this account but I have not had access to it. Silloway described these pavements as "dirt or clods or fragments of cow-chips." The pavements noted by Peabody were of "gumbo," of which "2 or 3 bits" were used at one nest and 40 at another. A third had "cow-chips." Silloway and Peabody's accounts (in Montana and Wyoming) referred to *O. a. leucolaema.* Mouseley (1916) was the first to record a "pavement" for *praticola.* He describes it as of cow-chips and (another nest) of flat pebbles or stones. In most of the photographs of nests accompanying this article a "paving" is visible and in others it is present but the separate items have been obliterated by rain. In my opinion practically all nests of *praticola* have this pavement though it may vary considerably in shape, size and number of items. See Tables 5 and 6 for an account of the details of this interesting structure at all of the nests at Evanston and Ithaca.

Mouseley (1916) suggests that the Lark uses for "paving" that which is best suited, thus: "As regards the paving it [the bird] seems to have displayed that marvelous instinct which birds seem at times to be endowed with, for instead of using cow-chips as a paving which, in such a wet, spongy place would have been of little good, it resorted to the use of very thin and flat stones." In my opinion the bird uses what is most accessible—at Evanston clods, at Ithaca pebbles—and shows no prescience whatsoever in the matter. If it does why should it have used clods almost exclusively at Evanston which the first rain would beat down and wash together when, by going a trifle further, it could have had an admirable assortment of pebbles left by the sidewalk contractors? Probably clods, formed by the drying of the surface that follows rains on the barren areas that the Lark inhabits, constitute the chief materials for "pavements" of *praticola.* That they have not been recorded more frequently is easily explained: a single rain obliterates a clod pavement and, moreover unless attention be called to it, even a freshly laid pavement may be overlooked. Thus a photograph of a nest taken by Allen (1925) at Ithaca, shows a good pavement but he had not noticed it until the writer called his attention thereunto. And again a meager pavement appears in a photograph by Wm.

TABLE 7

Material, sizes and weights of the nests of the Prairie Horned Lark at Evanston, Ill., 1926

Nest No.	Date Completed*	Materials			Measurements (centimeters)				Weight in grams
		Amount	Body of nest	Lining	Top ext. dim.	Top int. dim.	Depth inside	Depth overall	
1	March 22	Much	Stems and leaves of blue grass (*Poa pratensis*)	Fine grass, heads of aster					21.3
3	April 11		(No record)		8.4	6.6	5.5	6.4	
4	April 12		(No record)		9.1	7.1	4.6	5.9	
5	April 12		(No record)		8.1	6.6	4.8	6.3	
7	April 13		(No record)		8.6	6.4	4.5	6.1	
8	April 13		Fine grass only (*Poa pratensis*)	Aster heads, grass leaves	8.9	5.8		7.1	
9	April 13		Grass stems and leaves	Feather, paper bits, fine grass stems and leaves	9.6	6.7	3.8	6.1	
10	April 13	Much	Coarser stems, leaves, some dirt	Aster heads, plant fibers	9.6	7.6	4.1	5.8	12.1
11	April 14		Grass leaves, stems	Fine roots, aster heads, grass leaves	8.8	6.4	5.9	7.4	
12	April 14		(No record)		9.2	6.7	4.1	5.1	
13	April 26	Medium	A few fine roots, grass leaves, weed stems	Aster heads, grass leaves	7.6	6.4	4.6	6.4	9.4
14	April 27		(No record)		10.1	7.5	5.0	6.7	
15	May 3		(No record)		8.6	6.7	5.0	6.3	
17	May 9	Medium	Fine grass only	Grass leaves, aster heads	8.0	6.6	5.1	7.1	
18	May 21	Much	Grass stems and leaves, few fine roots	Fine plant fibers, grass leaves	8.9	7.1	4.8	6.7	14.7
19	May 22		*Setaria* leaves, scrap of cloth	Paper, leaves of *Setaria*, plant fibre, string	9.1	6.7	4.8	6.1	
21	June 9	Small	Stems of *Setaria*, other coarse material, much dirt	Same as body	8.6	6.9	4.8	5.9	14.9
22	June 17	Small	Some roots, stems and leaves of grass, dirt	Paper, heads of aster	8.9	7.4	3.0	5.8	10.1
23	June 22	Much	Roots, coarse stems and weed leaves, much dirt	Same as body	9.2	7.8	4.8	6.3	24.4
24	June 27	Much	Coarse weed stems and leaves, a few roots, dirt	Same as body	8.4	6.7	4.6	5.8	15.4
				Average:	8.62	6.87	4.65	6.27	15.28

*Estimated.

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P. Chandler (Sutton, 1927, p. 139) and a rather extensive one in a beautiful photograph by Frank Pagan (Forbush 1927, pp. 356-357). Likewise, I do not hesitate to say that if I had not had Peabody's article in mind at the time the nests were found I might never have noted, in the field, these structures which seem so obvious in the photograph.

The purpose of pavements seems clear. Though it may serve as a decoration, a concealing structure or in some such capacity as is attributed to snake's exuviae or rags found at other birds' nests, I believe its origin can be traced to two things: (1) the method of building the nest and (2) the Lark's persistent demand for bare surfaces upon which to walk. Under the first point it should be remembered that the excavation is built back under an object on one side and has a long slope on the other. Nest material is not laid out to level up this slope but the pavement is (see Figure 10, also Plate VI, Fig. 2 and Plate VII, Fig. 1). Though Mouseley has shown, in one case, that the pavement was entirely laid before any nesting material and Figure 10 would not correspond exactly with his description, yet the purpose of the pavement could be the same in either case. And, too, a study of the construction of many nests seemed to show, that in some cases at least, pavement is laid after the nest is completed for much of the paving was above and over the outer edges of the nest material. The demand for a bare approach to the nest and the consequent laying of a pavement to cover up intervening grass or nest edges seems to constitute another reason for this interesting structure. To substantiate this see Plate X, Fig. 2; Plate XI, Fig. 2; Plate XII, Fig. 2; Plate XV, Fig. 2. And some nests which had bare ground on all sides had no appreciable "pavement" (Plate XIV, Figure 2 and Plate XV, Fig. 1). But, in order that the theory may not be too perfect, some nests which were surrounded by grass and should, under this hypothesis, have had the most extensive pavement had perhaps not more than a single, insignificant item (see Plate XVII, Fig. 1). In concluding it should be remarked that the Larks, if undisturbed, invariably approach the nest over the pavement (see Plate XXVIII, Figure 2).

Eggs and egg-laying.—The egg of the Prairie Horned Lark has been described over and over in the evolution of ornithology from the "science" of oölogy. But, as far as I know, no one

TABLE 8

Material, sizes and weights of the nests of the Prairie Horned Lark at Ithaca, New York, 1927

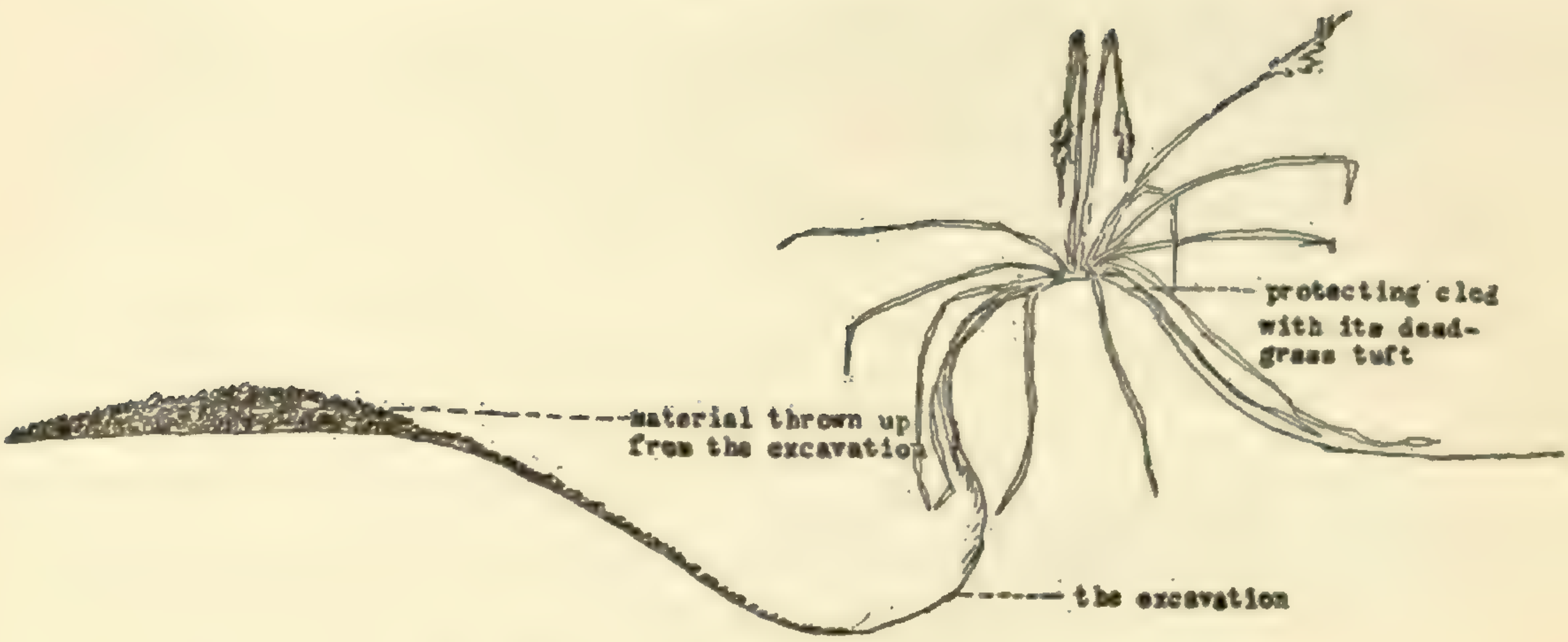
Nest No.	Date Completed*	Materials			Measurements (centimeters)				Weight in grams
		Amount	Body of nest	Lining	Top ext. dim.	Top int. dim.	Depth inside	Depth overall	
B_1	March 15.....	Much.....	Weed stems, fine roots, dirt.....	Fine roots.....	7.6 by 8.9	5.1 by 5.8	3.8	5.8	10.7
A_1	March 20.....	.....	Weed stems, dirt, fine roots.....	Aster heads.....	9.6 by 10.2	5.8 by 7.1	3.5	5.3	10.1
B_2	April 8.....	Medium....	Stems and leaves of *Setaria*, a few fine roots.	Same as body.....	7.6 by 10.5	5.1 by 5.5	4.5	4.8	7.9
A_2	April 22.....	Small.....	Coarse stems of *Setaria*, a few fine roots, much dirt.....	Several feathers.....	8.3 by 10.2	6.4 by 7.1	3.8	5.1	12.0
B_3	June 4.....	Much.....	Fine roots and leaves of rye.....	Same as body.....	7.6 by 9.6	5.8 by 6. 9	3.8	4.5	8.7
				Average:	8.14 by 9.88	5.64 by 6.48	3.88	5.10	9.88

*Estimated.

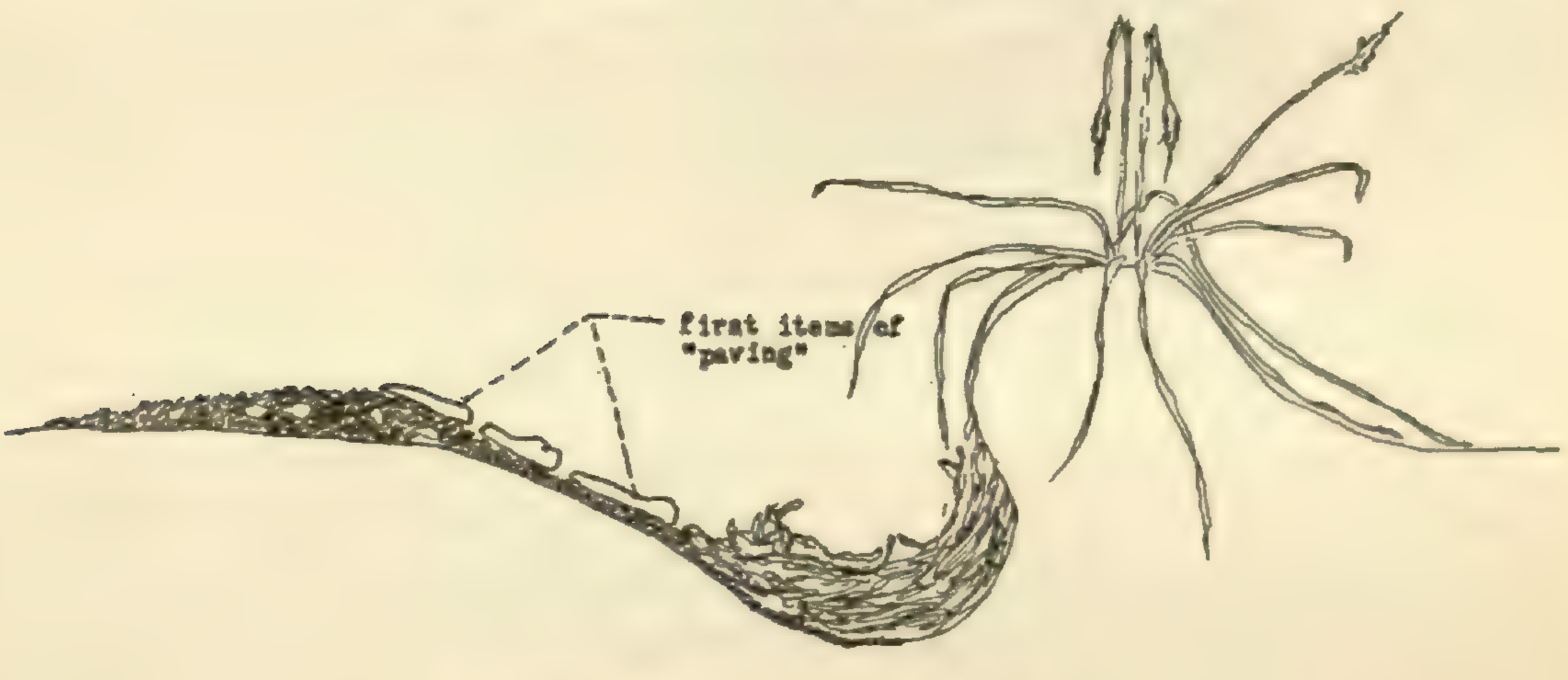
has compared the color with Ridgway's (1912) standards. On this basis the egg may be described as elliptical, rather unusually pointed for a Passerine bird, with a ground color of grey or, occasionally, with a greenish tinge. The spotting is fine, uniform, almost completely concealing the background, and is cinnamon-brown in color. The eggs are quite uniform but many have a denser ring of pigment about the larger end (see Plate XVI, Fig. 2). Saunders (1899), describes in *Otocoris alpestris flava* of Europe occasional "hair-lines" about the larger end. One case of this was observed in *praticola* (see Plate XVI, Fig. 1). Another interesting color variation was that of a single egg in two nests of the "B" female (nests B_2 and B_3). Here a deficit of pigment caused the egg to show more background than normal (see Plates IX, Fig. 2, and XVIII, Fig. 2). It was probably the fourth and last egg laid for it was the last to hatch. Nest B_1 had but three eggs so this type of coloration did not appear in it. Incidentally this egg, as well as the characteristic actions of the bird, made positive the identity of the owner of the nests and confirmed the evidence of the territory.

There is but little of significance in an egg measurement, still twenty-two eggs of nine different nests were measured. The average length of the twenty-two was 2.25 cm., the average width 1.55 cm. The smallest was 2.13 by 1.46 cm., the largest 2.45 by 1.58 cm., the longest 2.45 cm., the shortest 2.13 cm., the broadest 1.66 cm., the narrowest 1.46 cm. Mouseley (1917), in his study of second sets, found a considerable descrepancy in size (.82 by .58 inch average first set as opposed to .78 by .58 inch average, second set). My results are the reverse of this. A single egg of Nest A_1, laid about March 15, measured 1.58 by 2.13 cm., three eggs of nest A_2, laid between April 21 and 23, were all of the same measurement, viz., 1.58 by 2.22 cm.

The number of eggs per set varies from two to five ordinarily, though Levy (1920) records a most exceptional case of eight eggs in a nest. March nests have the smaller sets, usually two or three. Five nests of two eggs, eleven of three, eleven nests of four, five nests of five, made up the sets of the nests at Evanston and Ithaca. Some of these, of course, had hatched before the nests were found. There is probably a close relationship between temperature and small sets in March (sets of five occurred only in late April, May and June). Nine eggs of five sets at



The Nest-excavation in Cross-section



Nest Foundation with First "Paving" items

Completed Nest and "Paving"

Fig. 10. The construction of the nest of the Prairie Horned Lark, with an explanation of "pavings".

Evanston averaged 2.19 cm. by 1.50 cm. The thirteen eggs of four sets at Ithaca averaged 2.28 cm. by 1.59 cm. Whether there is any significance in this discrepancy I cannot say. Though Ithaca eggs were larger, on the other hand, Evanston nests were larger. Probably both discrepancies would disappear in a large series.

The actions of the adult birds during egg laying have already been discussed under nest-finding. More need not be said here except that the actions of the female at this period are those of a bird with an infinity of leisure, patience and unconcern. She does nothing but remain quietly in one place, forever preening herself. The male at this time, attends her as assiduously as a groom. Now frequently incubation begins before the set is complete but the actions of the female then constitute another matter.

Incubation period.—Forbush (1927) gives the following periods of incubation: 12 days (H. O. Green); 11 days (L. McI. Terrill); 14 days (A. W. Butler). Jones (1892) puts the average at 13 days and says, "I doubt if any eggs are hatched in less than 12 days." As already has been noted no nest was followed from the time of the first egg to hatching, but in three instances the last egg was laid after the nest was found. This last egg, or the last young which was most probably of this egg, hatched on the 12th day after laying, in the three cases. From the time of laying to the time of hatching about eleven days would have intervened. The incubation period determined by MacDonald (1916), for *O. a. leucolaema*, was in exactly the above fashion; a fourth egg was laid after a nest with a set of three was discovered. All hatched within twenty-four hours of each other, eleven days from the laying of the last egg. Her conclusions that incubation extends from eleven to fourteen days is unwarranted, however, for it is at once obvious (since all hatched together), that incubation did not begin until the last egg was laid. At Evanston, however, the last to hatch was often a full day behind all the others in many of the early sets, that is, three would hatch within an hour or two of each other, the fourth almost exactly twenty-four hours later. No other conclusion is logical but that incubation began the day before the last egg was laid (the nest was found because the bird had begun to incubate) and that eleven days is the period for all.

TABLE 9

History of the successive nests of territories A, B and C at Ithaca, New York, 1927

Nest No.	Date Completed*	No. of eggs	Position in territory	Distance from former nest	Fate
A_1	March 20.....	2	East center.....	.....	Destroyed by snow.
A_2	April 22.....	3	West center.....	85 yards.....	Three young successful.
B_1	March 15.....	3	South margin.....	.....	Destroyed by low temperature and snow.
B_2	April 8.....	4	West center.....	110 yards.....	One young only successful.
B_3	June 4.....	4	West margin.....	40 yards.....	Destroyed by Cowbird experimentation.
C_1	April 21.....	5	East margin.....	.....	Three young successful.
C_2	May 28.....	?	Nest not located....	Not known.....	Three young, at least, successful.

*Estimated.

Bergtold's (1917) record of 11 to 14 days is given on the authority of MacDonald. In one case in the writer's experience incubation extended for a known period of fourteen days but for some unknown reason the nest was deserted, apparently, for two days after incubation had begun (the eggs were cold), and this probably accounts for the unusual period. Considering eleven

TABLE 10

Reactions of the Prairie Horned Larks to man when eggs were in the nest, at Evanston, Ill., 1926.

Nest No.	No. of Visits	No. of Times Parent Noted	No. of Casual Abandonments	No. of Distress Simulations	No. of Other Reactions
3	9	5	1	2	2
5		4	0	1	3
6	5	5	4	0	1
7	9	6	2	2	2
8	4	3	1	1	1
9	14	8	7	0	1
10	11	5	4	0	1
11	10	8	1	5	2
12	8	6	3	1	2
13	10	8	3	1	4
14	11	8	5	1	2
15	11	11	5	0	6
19	11	8	6	1	1
20	5	4	3	0	1
21*	12	10	8	0	2
24	6	6	6	0	0
Total.....	142	105	59	15	31

*Experiments of June 20 at this nest not included; for these see table 14.

days the optimum I have used it as the basis for estimation of all the tables and figures where dates of egg-laying and nest-building are given.

Though Bendire (1895) and Criddle (1917) say the male assists in incubation (Criddle does not specify incubation but says "relieving the female upon the nest"), I have no good evidence that the male ever incubates or broods. I have determined the sex upon hundreds of visits to many different

TABLE 11

Reactions of the Prairie Horned Larks to man when young were in the nest, at Evanston, Ill., 1926.

Nest No.	No. of Visits	No. of Times Parent Noted	No. of Casual Abandonments	No. of Distress Simulations	No. of Other Reactions
3	11	7	4	1	2
4	7	3	1	0	2
5	7	5	0	2	3
7	11	8	1	0	7
9	10	6	4	0	2
10	11	1	1	0	0
11	10	3	3	0	0
12	9	2	0	0	2
13	11	5	2	0	3
14	11	9	2	1	6
15	10	7	0	0	7
19	3	2	1	1	0
20	19	11	6	1	4
21	9	5	0	1	4
22	9	9	3	0	6
Total.....	148	83	28	7	48

TABLE 12

Reactions of the Prairie Horned Larks to man when eggs were in the nest, at Ithaca, N. Y., 1927.

Nest No.	No. of Visits	No. of Times Parent Noted	No. of Casual Abandonments	No. of Distress Simulations	No. of Other Reactions
A_1	11	2	2	0	0
A_2	11	7	6	1	0
B_1	2	2	0	1	1
B_2	6	5	0	4	1
B_3	4	3	0	2	1
C_1	8	5	4	0	1
D	6	4	4	0	0
Total.....	48	28	16	8	4

nests and always it has been the female. A full day spent at one nest (Table 15), failed to show the male in any inclination to incubate. Similarly a full day at a nest with young (Table 17) failed to show that the male broods.

Reactions of female and male Larks during incubation period.—The reactions of the incubating female express some of the most highly-developed nest-protective instincts among birds. She has two such instincts with a series between these two. The first, and most highly developed, is a reaction I have called

TABLE 13

Reactions of the Prairie Horned Larks to man when young were in the nest, at Ithaca, N. Y., 1927.

Nest No.	No. of Visits	No. of Times Parents Noted	No. of Casual Abandonments	No. of Distress Simulations	No. of Other Reactions
A_2	9	3	1	0	2
B_1	4	4	0	1	3
B_2	30	16	4	9	3
B_3	8	6	0	1	5
C_1	30	11	4	0	7
Total.....	81	40	9	11	20

the "casual-abandonment". Typically expressed it consists of an abandonment of the eggs while an intruder is from one-hundred to twenty-five yards distant. The female leaves without a sound (usually flying directly from the nest in spite of frequent remarks in the literature to the contrary), flies low against the ground like a grey wraith and is soon lost to sight. Her flight under such circumstances is unique and distinct, most frequently without marked undulation, with steady wing beat with a pause of time of about one beat between each beat. So highly developed is this method of nest protection that the female leaves the nest at a greater distance than a timid Lark would flush under other circumstances. Other writers describe this reaction though make no attempt to explain it. Thus Merrill (1888) in writing of *O. a. strigata* says: "The male, who is constantly on the watch, seems to call the female off the nest when an intruder is still at a distance; several times I saw one approaching her mate, shak-

ing her feathers and having evidently just left the eggs, but my efforts to flush one off the nest were fruitless. . .'' I do not believe the male influences the female in any way, she had gone from her nest at so great a distance that Merrill had not seen her leave. Brewster (1894) writes that the female sneaked off when at some distance, unconcerned, flew with a steady, rapid motion of the wings. Bendire (1895) quotes Harris: ''Early in the day the female will usually leave before you are within 50 yards of it, creeping away for some distance, crouched close to the ground before taking wing. . . Toward evening they are not so cautious, and very often the nest can be approached within a few feet . . . the female will fly only a few yards, alight, and begin pecking the ground. . .'' Brooks (1899) writes that the female ''flies straight away when one comes within 50 feet'' of the nest. Jones (1892), Hegner (1899) and Forbush (1927) describe a similar reaction as does Sutton (1927, p. 138) though the latter adds a bit of nonsense with the statement that, ''Perhaps the birds realize that human beings are acquainted with the crippled wing ruse of such species as the Killdeer and have decided to use other tactics''. Jones (1892) also presumed that Larks never went ''fluttering and crying'' from the nest. As a matter of fact Lark and Killdeer respond very similarly (for this see further and also the author's paper ''Nesting of the Killdeer'' cited below).

The other reaction is a marked distress simulation in which the female flushes only after an intruder is well upon the nest. She goes then calling and fluttering over the ground at a rapid run, horns up, wings flapping. Audubon (1832) describes this for both the male and female of *O. a. alpestris* and Forbush (1927) writes that ''sometimes when the eggs are near hatching, and she is suddenly surprised while incubating, she may act like a crippled bird. . .'' My observations have shown no clear relationship between this reaction and state of either incubation or brooding.

As Harris (Bendire 1895), has said, the nest may be more closely approached near night. In other words the typical casual-abandonment is best expressed during the lighter portions of the day and especially during the warmer days. Distress simulation, on the other hand, is more likely to be demonstrated near dark, on cold days, or if the incubating bird is approached

from the north so that the nest protection conceals the intruder until the nest is nearly under foot. But there are many variations. Some birds gave distress simulations under many circumstances, others gave nothing but casual abandonments. A complete graduation between these two reactions, of course, existed: the bird would allow close approach at times then leave without distress simulation, or fly but stay near and call. The unconcerned "ground picking" was always a sign of an incubat-

TABLE 14

Nest protective reactions of an incubating female Prairie Horned Lark (nest No. 21, June 20, 1926, Evanston, Ill.).

Time of Flushing Female	Interval Between Flushings	Time of Return	Interval Between Return and Flushing	Reaction
4:20 a.m.	.....	4:30 a.m.	.....	Casual abandonment
6:25	2 hours 5 minutes	.....	1 hour 55 minutes	Casual abandonment
6:35	10 minutes	6:38	.....	Distress simulation
7:44	1 hour 9 minutes	7:49	1 hour 6 minutes	Casual abandonment
12:40 p.m.	4 hours 56 minutes	12:45 p.m.	4 hours 51 minutes	Casual abandonment
3:09	2 hours 29 minutes	3:14	2 hours 24 minutes	Casual abandonment
3:20	11 minutes	3:26	6 minutes	Casual abandonment
3:36	16 minutes	3:41	10 minutes	Casual abandonment
3:42	6 minutes	3:45	1 minute	Distress simulation
3:47	5 minutes	3:53	2 minutes	Reluctance plus casual abandonment
3:57	10 minutes	4:01	4 minutes	Reluctance plus casual abandonment
4:06	9 minutes	4:11	5 minutes	Reluctance plus casual abandonment
4:11	5 minutes	4:14	0 minute	Reluctance plus distress simulation.
4:14	3 minutes	4:17	0 minute	Reluctance plus exaggerated distress simulation.
4:17	3 minutes	4:20	0 minute	Reluctance plus exaggerated distress simulation.
4:22	5 minutes	4:24	2 minutes	Reluctance plus casual abandonment.
4:30	8 minutes	4:35	6 minutes	Casual abandonment
4:46	16 minutes	4:53	11 minutes	Casual abandonment
5:01	15 minutes	.....	8 minutes	Casual abandonment
6:30	1 hour 29 minutes	.....	.....	Casual abandonment

Summary: Number of flushings: 20

Average length of time consumed in return of female to nest: 4:70 minutes.
Reaction when flushed immediately upon return: exaggerated distress simulation.
Reaction when flushed one minute from time of return: distress simulation.
Reaction when flushed two to five minutes from time of return: reluctance to leave plus ultimate casual abandonment.
Reaction when flushed five minutes or more from time of return: normal casual abandonment.

ing female. The male, beyond occasional call notes, showed little or no solicitude while eggs were in the nest.

To see if these two reactions, "casual abandonment" and "distress simulation", could be reduced to a formula I spent the greater portion of one day flushing an incubating female from her nest. The results are given in Table 14. Let me add that, in spite of this evil treatment, the eggs hatched in normal time, the young prospered until found by a weasel or other enemy. Moreover, I have tabulated the recorded reactions for every visit to incubating females both at Evanston and at Ithaca. These results are given in Tables 10 and 12. The "other reactions" here include intermediate types chiefly. Thus it will be seen that, though the first effort of a female Lark to protect her nest is to attempt to deceive the searcher by an unconcerned flight (the "casual abandonment"), this highly developed instinct is inhibited by various conditions (such as flushing at too close intervals), and then the more primitive instinct, that of distress simulation, gradually takes its place. In many respects these reactions resemble those of the Killdeer (see Pickwell, "Nesting of the Killdeer", Auk 42, 1925, pp. 490-491).

It has been my intention since beginning work with the Prairie Horned Lark to see if the above reactions would be given for animals other than man and if they were the same (or different), to speculate upon the reasons. No opportunity has as yet presented itself for this type of experimentation but two accounts in the literature give a clew. Brooks (1908) writes that adult Larks at French Creek, West Virginia, alighted on the backs of chickens to drive them away from the nest. Criddle (1920), also remarks that the female Lark would fly at a hen with such vigor as to cause her to become seriously alarmed and to make her leave in a hurry. Criddle also makes the important observation that before *dogs* and man the female slipped quietly from her nest. This last was, apparently, a typical abandonment concealment. It appears, then, that the Lark does not reserve a special reaction for man alone but can, however, distinguish between mammals and large birds and has distinct reactions for each.

The Young

Hatching.—Of hatching there is but little to say. In spite of daily visits only once did I arrive during hatching, once only

TABLE 15

A day's activity of the male Prairie Horned Lark during the incubating period (nest No. 21, June 20, 1926, Evanston, Ill.)

Time of Day	
4:20 a.m.	Nest reached. Male not in vicinity.
4:53	Within 50 feet of nest.
4:54	Intermittent ground song.
4:59	Intermittent ground song, 50 feet from nest.
5:25	Greeted female as she left nest.
5:30	Recitative ground song, 30 feet from nest.
5:33	Intermittent ground song from southeast song post, 90 feet from nest.
5:55	Intermittent ground song and calls, 50 feet from nest.
6:00	Sitting quietly on mound, 30 feet from nest.
6:05	Came within 2 feet of nest.
6:14	Intermittent ground song, 30 feet from nest.
6:15	Flew from vicinity.
6:44	Intermittent ground song, 150 feet southeast of nest.
6:47	Still singing as previously.
7:03	Singing as previously.
7:12	Intermittent ground song, 50 feet due east of nest, sang here 3 minutes.
7:17	Intermittent ground song, 150 feet southeast of nest.
7:24	Soft intermittent ground song, 25 feet due east of nest.
7:25	Remained within 20 feet of nest while female was away.
7:33	Intermittent ground song, 150 feet southeast of nest.
8:00	Intermittent ground song, 240 feet south of nest.
8:06	Intermittent ground song, 60 feet southeast of nest.
8:09	Soft intermittent ground song, 30 feet east of nest.
8:11	Within 6 feet of nest.
8:21	Singing near.
8:25	Intermittent ground song, 30 feet east of nest.
8:29	Calling.
8:31	Flew from vicinity.
9:00 to 9:59	During my efforts to photograph female, male remained near, singing.
10:03	Flight song.
10:15	Intermittent ground song, 25 feet east of nest.
10:16	Intermittent ground song south of nest.
10:40	Intermittent ground song, 150 feet southeast of nest.
11:39	Intermittent ground song near nest.
12:43 p.m.	Flight song.
12:55 to 1:00	Intermittent ground song, 150 feet southeast.
2:00	With female, calling, 30 feet east of nest.
2:47	Ground recitative, 150 feet southeast of nest.
3:24	Intermittent ground song, 90 feet south of nest.
3:30	Intermittent ground song, 150 feet southeast of nest.
3:46	Intermittent ground song, 50 feet east.
3:51	Intermittent ground song, 225 feet south of nest.
4:40	Recitative ground song, 90 feet south of nest.
4:53	Intermittent ground song, 300 feet south.
5:01 to 6:30	(Interval out for observations of other Lark nests.)
6:39	Flight song.
7:33	Quiet, 150 feet southeast of nest.
7:37	Evening recitative.
7:40	Still singing evening recitative.
7:50	Quiet, 300 feet south of nest.

Summary:

Song posts

Song records at 25 feet from nest:	3
Song records at 30 feet from nest:	6
Song records at 50 feet from nest:	5
Song records at 60 feet from nest:	1
Song records at 90 feet from nest:	3
Song records at 150 feet from nest:	8
Song records at 225 feet from nest:	2
Song records at 300 feet from nest:	2
Average distance	116 feet, or 38.66 yards

Song types

Periods of ground intermittent:	28
Periods of ground recitative:	5
Flight songs:	3
Total song periods	36

while empty shells were yet in the nest and but once or twice before the newly hatched were completely dry. The egg breaks about the larger end, the young emerges, the parent promptly removes the empty shell, the down soon drys and within an hour or two, perhaps much less, the nestling supports himself upon his belly and wing tips, cranes his neck toward the zenith and opens wide a yellow-patched maw.

Feedings.—The most important thing in the life of a nestling is food and this is supplied, as a rule, by both parents. In

TABLE 16

Observations of the incubating Prairie Horned Lark Female (nest No. 21, June 20, 1926, Evanston, Ill.)

Time of Day	
4:20 a.m.	Flushed with casual abandonment at 30 feet.
4:30	Returned to nest facing southwest.
4:45	Faced northeast.
5:12	Faced southwest.
5:25	Left nest.
5:26	Returned to nest. Flew within 4 feet, walked in.
5:41	Faced northeast.
5:45	Flew from nest, alighted 60 feet away.
5:53	Returned to nest vicinity, dug out a cut worm near nest.
5:55	Returned to nest, faced southwest.
6:09	Turned eggs, faced northeast.
6:10	Faced southwest.
6:20	Faced northeast.
6:38	Faced southwest.
6:47	Faced northeast.
6:54	Left nest.
6:55	Returned to nest, walked in from 30 feet.
7:25	Left nest.
7:31	Returned to nest, walked in from 30 feet, picked ground.
7:34	Faced southwest.
7:42	Faced northeast.
8:03	Left nest.
8:10	Returned to nest, walked in from 30 feet.
8:11	Faced northeast.
8:38	Faced southwest.
8:42	Left nest, flew 100 yards away.

(Remainder of day spent in photography and experimentation.)

one or two cases I failed to see the male with food at any time but usually he did about as well as the female. In the case of the feedings recorded in Table 17 the male visited the nest less often than the female but he usually came with a much greater burden, fed more nestlings, so that, all in all, the case was about even between them. For an extensive record of feedings see Table 17. This account is for April. Shorter observations in June and July gave similar records. It has not been possible, as yet, to determine whether or not the rate of feeding varies with the age of the young, or just when the male begins to

TABLE 17

Table of feedings, and other activities of the Prairie Horned Lark (nest No. 7, for April 30, 1926, at Evanston, Ill.).

Time of Feeding	No. of Nestlings Fed	Reaction to Excreta	Interval Between Feedings in Minutes	Sex Feeding	Brooding Periods
5:14 a.m.	1	Removed		Female	
5:21.5	1	Removed	7.5	Female	
5:47	1		25.5	Female	Brooded
6:03	2	Removed	16	Female	
6:12			9	Female	Brooded to 6:37
6:44			32	Female	Brooded
7:09		Removed	25	Female	
7:16		2 eaten	7	Female	Brooded
7:37			21	Female	
7:42	1		5	Female	
7:45	1		3	Female	Brooded
8:04	1	Removed	19	Female	
8:06	1		2	Female	Brooded
8:17	1	Removed	11	Female	
8:25	1		8	Female	Brooded
8:38	2		13	Female	
8:45.5	1		6.5	Female	
8:51	1		6.5	Female	Brooded
8:56	1	Removed	5	Female	
9:00	1		4	Female	
9:02.5	2		2.5	Female	
9:09	1		6.5	Female	
9:12			3	Male	
9:19	2		7	Male	
9:26	1	1 eaten	7	Female	
9:34	1	1 eaten	8	Female	
9:34.5	3		0.5	Male	
9:40	1		5.5	Female	Brooded
9:44	1		4	Female	
9:51	1		7	Female	
9:52	2	1 eaten 1 removed	1	Male	
10:01	2		9	Male	
10:03		eaten?	2	Female	Brooded
10:10	1		7	Female	Brooded
10:17	2	1 eaten	7	Male	
10:29	1		12	Female	
10:31		1 eaten	2	Female	Brooded
10:33	2	1 eaten	2	Male	
10:37	1		4	Female	Brooded
10:43	1		6	Female	Brooded
10:44	2	1 eaten	1	Male	
10:52	2		8	Male	
10:52.5			0.5	Female	
11:00	3		7.5	Male	
11:01			1	Female	Brooded
11:02			1	Female	
11:05	1		3	Female	
11:12	1	1 eaten	7	Female	
11:14	2		2	Male	
11:24	1		10	Female	Brooded
11:34.5	1		9.5	Female	
11:41		Removed	6.5	Female	
11:42			1	Male	
11:52.5	1		9.5	Female	
11:55	4		2.5	Male	
11:58			3	Female	
11:59	3		1	Male	
12:05 p.m.			6	Female	Brooded
12:11	2		6	Male	
12:18	3		7	Male	
12:20	1		2	Female	
12:26	2		6	Male	
12:32	1	1 eaten	6	Female	
12:38			6	Male	
12:45		2 eaten	7	Female	
12:46	1	1 eaten	1	Male	
12:50	2		4	Female	

TABLE 17—Continued

Time of Feeding	No. of Nestlings Fed	Reaction to Excreta	Interval Between Feedings in Minutes	Sex Feeding	Brooding Periods
12:57	1	.....	7	Female.....	.....
12:59	.....	.....	2	Male.....	.....
1:02	2	.....	3	Female.....	.....
1:17	2	.....	15	Male.....	.....
1:20	1	.....	3	Female.....	.....
1:45	.....	2 eaten.....	25	Female.....	Brooded
2:09	1	.....	24	Male.....	.....
2:14	1	Removed.....	5	Female.....	.....
2:18	2	Removed.....	4	Female.....	.....
2:30	1	Removed.....	12	Male.....	.....
2:37.5	1	.....	7.5	Female.....	.....
2:44	1	Removed.....	6.5	Female.....	.....
2:51	.....	.....	7	Female.....	.....
2:59	1	.....	8	Male.....	.....
3:03	.....	1 eaten.....	4	Female.....	.....
3:09	1	.....	6	Female.....	.....
3:12	.....	.....	3	Male.....	.....
3:14	1	Removed.....	2	Female.....	.....
3:28	.....	.....	14	Female.....	.....
3:31	.....	.....	3	Male.....	.....
3:33	.....	.....	2	Male.....	.....
3:33	.....	.....	0	Female.....	.....
3:34	.....	1 eaten.....	1	Female.....	.....
3:38	1	1 eaten.....	4	Female.....	.....
3:40	.....	.....	2	Male.....	.....
3:43	.....	.....	3	Female.....	Brooded
3:48	.....	.....	5	Male.....	.....
3:52	1	1 eaten.....	4	Female.....	Brooded
3:53	2	.....	1	Male.....	.....
4:02	3	.....	9	Male.....	.....
4:10	1	1 eaten.....	8	Male.....	.....
4:17	.....	.....	7	Male.....	.....
4:20	1	.....	3	Female.....	Brooded
4:25	3	.....	5	Male.....	.....
4:43	1	.....	18	Female.....	Brooded
4:54	.....	.....	11	Male.....	.....
5:01	.....	.....	7	Male.....	.....
5:03	1	.....	2	Female.....	Brooded
5:04	.....	.....	1	Female.....	Brooded
6:54*	.....	.....	.....	Male.....	.....
6:55	.....	.....	1	Male.....	.....
7:00	.....	.....	5	Male.....	.....

*One hour and fifty minutes interval just preceding for the daily tabulation of other Lark nests.

NOTE: After 2:21 p.m. a radical change of temperature took place. The temperature reached a maximum of 87 degree F. fell immediately thereafter 27 degrees in fifteen minutes and 35 degrees within an hour (the greatest fall, for so brief a time, in the Chicago region). This accounts for the frequent brooding of the female from 3:43 p.m. and the disproportionate feedngs in favor of the male.

Summary:

Extent of time of actual observation	11 hours 46 minutes
Extent of feeding time	13 hours 36 minutes
Total number of observed feedings	108
Total number of feedings, estimated	117
Number of observed feedings by female	69
Number of observed feedings by male	39
Average interval between feedings	6.53 minutes
Average interval with both sexes feeding regularly (9:12 A.M. to 3:43 P.M.)	5.5 minutes
Average interval with female feeding alone (5:14 A.M.to 9:12 A.M.)	11.75 minutes
Average intervals of feedings of male when he was feeding nearly alone (3:40 to 5:01 P.M.)	10.0 minutes
Average interval between feedings by female from her first feeding to her last (5:14 A.M. to 5:04 P.M.)	10.28 minutes
Average interval between feedings by male from his first feeding to his last (9:12 A.M. to 7:00 P.M.)	12.25 minutes
Shortest interval between feedings	.50 minutes
Longest interval between feedings	32.00 minutes
Total number of young fed by female (estimating each period with no record as one nestling fed)	76
Total number of young fed by male	67

assist. Apparently the only other record of rate of feeding visits is that of Dibble (1900) who recorded twenty visits in an hour.

Food of nestlings.—Here is a field where more investigation would be profitable. General notions as regards the type of food are available but quantitative studies, of any extensive scope, are non-existant. I have identified the following food being carried to nestlings: Lepidopterous larvae (chiefly "cutworms"), earthworms (very frequently), grasshoppers, moths and seeds of *Setaria*. What little weed seed nestlings receive is given them in March and April, earthworms are favorites in April, cutworms in March, grasshoppers in June and July.

A few nestlings that had died of exposure in late March and April were collected and it was surprising to find their stomachs fairly well filled with food, as follows:

1. March nestling.
   Animal matter 100%
      Two fly puparia.....30%
      Beetle fragments 70%

2. March nestling.
   Animal matter 100%
      One "cutworm".....70%
      Beetle fragments 30%

3. March nestling.
   Animal matter 100%
      Two "cutworms".....70%
      One fly puparium..... 5%
      Beetle fragments 25%

4. April nestling.
   Animal matter 100%
      All beetle fragments.

McAtee (1905) examined stomachs of ten nestlings, found that those obtained earliest and in northern states contained the largest amount of vegetable matter. A New York nestling had been fed 45 per cent whole wheat grains. Among the vegetable matter was green foxtail *(Chaetochloa viridis)*, tumble weed *(Amaranthus)*, and yellow sorrel *(Oxalis stricta)*. The grasshoppers predominated in the animal matter, 41.5 per cent of all the food. Weevils came next. Other insects were wire worms *(Elateridae)*, white grubs *(Scarabaeidae)*, leaf beetles *(Chrysomelidae)*, and pill beetles *(Byrrhidae)*.

One of the most interesting things in connection with the food of nestlings is the method the parents, especially the female, employs in getting it. Much of it is dug up somewhat in the

manner in which a Robin secures earthworms. Thus I have seen the Larks dig up both cutworms and earthworms. McAtee (1905) quotes a correspondent in regard to this method of securing cutworms for the young. This correspondent, Dr. Le Baron, recounts the description of a farmer who watched the Lark pry out cutworms from beside the hills of corn, seeming to know, by some method, just where they were to be found, and taking one after another until four or five had been secured before leaving for the nest. Criddle (1920) describes a similar method used by *praticola* in Manitoba though in this case the cutworms were secured from the sides of scattered clumps of weeds.

Reactions of adults with young in nest.—The surprising thing in the reactions of the Larks at this period is not that they are so different from the reactions when eggs are in the nest but that the reactions are so similar. The female does much brooding during the first few days (especially in the case of early nests) following hatching and her solicitude is expressed in a fashion very similar to that exhibited during incubation. Later she does more calling, stays nearer, gives fewer casual abandonments. One female would invariably fly close above my head as I approached her nestlings, then as I sat near the nest she would stay near me and hunt for food within twenty to thirty feet and always, under such circumstances, approached the nest with great hesitancy. Again another went up into the air while I was by her nest and flew about for several minutes three or four hundred feet overhead and in circles two or three hundred yards in diameter. During this time she made not a sound. But these reactions were exceptional. Tables 11 and 13 give a summary of reactions of adults when young were in the nest. Casual abandonments and distress simulations persist but "other reactions," i. e., calls, flights above the nest, have greatly increased. The male shows concern for the first time after the eggs hatch, but then it is confined to calls. His solicitude for safety of the young is frequently non-existant. In such cases, if he is not timid, he will feed unconcernedly while an intruder is within a few feet, though the female with her highly developed concealing instincts may not approach the nest. If the male is timid he merely stays away from the vicinity until the intruder leaves.

Nest cleaning.—One of the most peculiar and at the same time most highly developed of instincts is that of nest sanitation. So highly developed it is that frequently it inhibits instincts of protection solicitude. Thus at one time a female was coaxing the last of her young from the nest, away from my presence, when she spied excreta in the *empty* nest. She promptly deserted her nestling, leaving it there near me, the offending enemy, picked up that dropping and flew away with it. Droppings carried away were usually removed fifty to one hundred feet, deposited, and the bill whetted thoroughly afterward. They could not be left near the nest. On one occasion the male flew up to an old cabbage stump near the nest with a bolus of excreta (Plate XXIX, Fig. 1). My camera shutter, trained on the stump, surprised him into dropping his burden. That accident inhibited his alarm, however, for he hopped down among the weeds at the base of the cabbage stump, hunted for a moment, found his dropping, then flew off with it. In March and April nearly all excreta was *eaten* by the adults; in June and July nearly all was carried away and dropped. There is here, very probably, a close connection between the variation in this habit in the various seasons, and the available food supply.

Developmental reactions of the young.—Why young birds have no fear at hatching and why this instinct and others should suddenly appear in them at a surprisingly definite period, cannot be fully explained. It is instinctive certainly, lying dormant however until the physical state of the nestling can carry out, logically, its promptings. The Larks reach the age of discrimination about twenty-four hours after their eyes are open, that is, on the fifth or sixth day. Prior to that time they will respond, i. e., open their mouths, at any sound, especially a whistle. Failure to respond, or discrimination, is not an instantaneous acquisition but becomes noticeable over a period of one or two days, at times three or four. Shortly after discrimination becomes apparent in the young they learn to withdraw at the touch of a hand and also there is the first evidence of an instinct for concealment, for then they remain wonderfully quiet in the nest. Also at this time, the seventh to ninth day, they learn the crouch-concealment for, upon being removed from the nest, they sit quietly upon any object upon which they may be placed though at any younger age they will struggle and wriggle.

Fear—stark, blatant, naked—does not disclose itself until the young are near nest-leaving age. This is a wise provision of nature certainly for otherwise fear would drive them from the nest at the approach of an alarming object before the proper time. Indeed fear and nest-leaving seem to be co-operative. I have noted that a nestling, a few hours prior to nest-leaving, would sit quietly in the hand, but a short time later, with the first trial of the legs outside the nest, would, when captured, struggle violently and squeal piteously. Having found their legs they also find the desire to use them for escape. Disease, starvation, improper development all retard this psychical growth. Thus one entire set, improperly nourished, responded up to the ninth day. In many nests one or more nestlings would, because they were from a few hours to a day younger, show a greatly retarded physical and psychical development from two to three days behind their more fortunate brethren. This was a result of the method of feeding (to be taken up later), whereby an advantage in age would permit the older young to secure most of the food (see Plates XXIII to XXVIII, inclusive).

Growth of the young.—Rather extensive data, collected in this field, have been reduced to tables and curves (Tables 18,

TABLE 18

Growth in grams of an April set of Prairie Horned Lark nestlings to nest leaving, Ithaca, N. Y., 1927.

Nestling No.	1	2	3	4
April 21	3.4	3.0	3.0	2.6
April 22	4.1	3.8	3.6	2.6
April 23	5.0	5.0	3.7 (lost)	2.2 (dead)
April 24	7.1	7.2		
April 25	8.7	8.3		
April 26	9.9	10.4		
April 27	11.2	9.0 (dead)		
April 28	13.2			
April 29	14.2			
April 30	16.3			
May 1	17.0			
May 2	18.1			
Av. daily increase	1.33	0.98	0.80	0.20

19, 20, 21, Figures 12, 13, 14, 15, 16, 17), and a brief summary only will be given here. There are but two or three measurements that have significance, as far as I can see, and these only have been considered, i. e., weight, total length, length of tail and length of flight feathers.

The weight of the egg near hatching averaged 2.85 grams. As might be expected the newly hatched Larks were a little less than this, but so promptly are they fed that very few first weighings were made before the young were able to show a

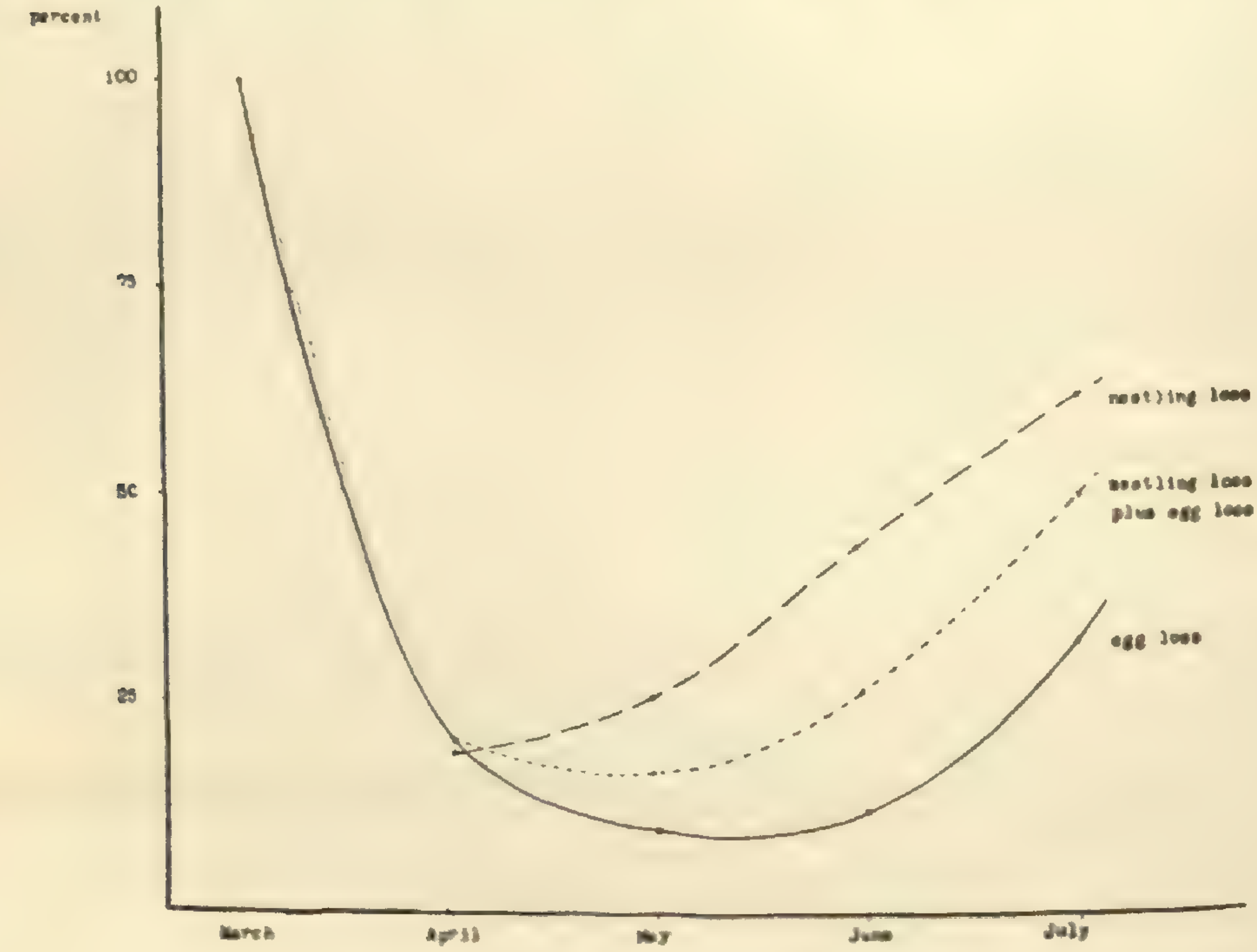


Figure 11

Fig. 11. Loss of eggs and nestlings of the Prairie Horned Lark during the 1926 nesting season at Evanston, Ill., in per cents per month.

considerable increase over the egg weight. Growth is uniform, both in weight and length, until the approach of the seventh day. At this time the rapid, very general unsheathing of the feathers causes a check in weight growth. Indeed a loss is shown where weighings were made late on the seventh day and early on the eighth (see Figure 13). The Cowbird nest-mate of one Lark nestling was still in pin-feathers at this period and does not show this straightening in the curve (see Figure 15). The April nestling developed so slowly that this straightening in the curve in its case (see Figure 12) is not apparent. As might be

expected, growth in length shows no lessening between the sixth and eighth days but rather an acceleration (see Figure 14). This is due to the advent of the tail. The retarded or lost young noted in the figures are, for the most part, the result of starvation through poor feedings and scanty food supply. The poor showing of the April nestling (see Figure 12) is an exaggeration of the situation that prevailed (though usually to a less degree) in most April nests. It is the result of two things: (1) prevailing low temperature and the consequent necessity of much

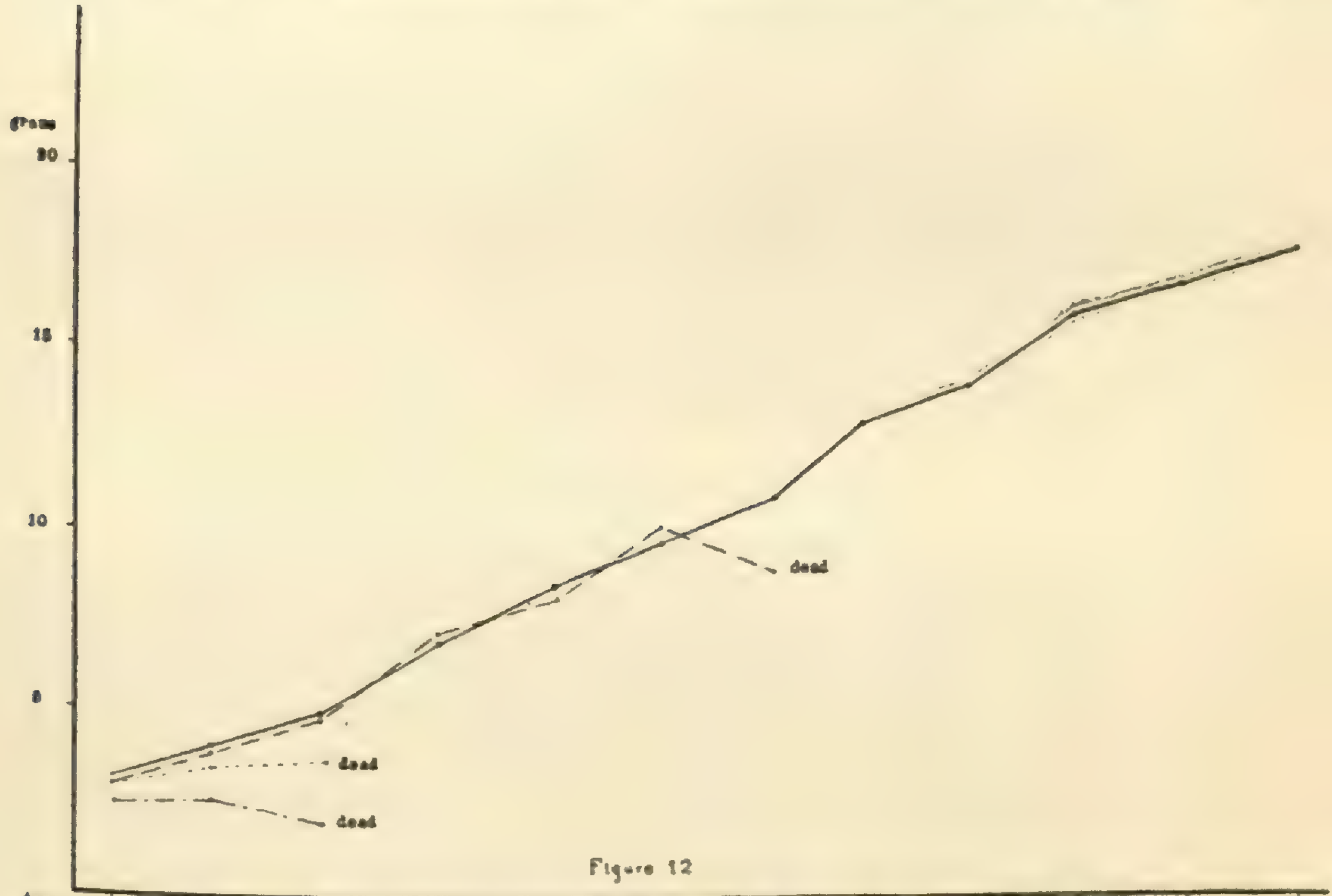


Figure 12

Fig. 12. Growth in weight of an April set of Prairie Horned Lark nestlings (nest B_2, April 21 to May 2, inclusive, Ithaca, N. Y., 1927).

brooding, hence lessened feedings (see Figure 16) and, (2) an apparent lower supply of food.

Attention should be called to one more point. In the general averages (Table 21) the lessened growth in weight and lessened increase in length between the tenth and twelfth days is due to the fact that birds in the nest at these ages are almost certain to be those retarded or improperly nourished, the most prosperous having gone on the tenth.

Descriptions of young at various ages.—The young in juvenile plumage have been described repeatedly, but apparently

TABLE 19

The Growth of a May set of Prairie Horned Lark nestlings from day of hatching to nest-leaving, Ithaca, N. Y., 1927

Nestling No.	Weight (in grams)					Length (in centimeters)				
	1	2	3	4	5	1	2	3	4	5
May 6	3.5	3.4	3.5	3.2	2.3	5.0	5.0	5.0	4.8	4.5
May 7	4.9	4.6	5.3	4.0	3.1	5.8	5.6	5.8	5.1	5.0
May 8	7.1	5.7	7.0	5.3	3.6	6.7	6.1	6.6	5.8	5.5
May 9	9.2	8.3	9.0	6.3	4.7	7.2	7.1	7.1	6.1	5.6
May 10	10.0	10.8	12.4	lost	5.8	7.4	7.5	7.2	lost	6.1
May 11	13.9	14.1	16.5	.....	6.0	7.8	7.8	8.1	.....	6.1
May 12	19.9	18.6	17.8	.....	9.0	8.9	8.6	8.8	.....	7.4
May 13	19.2	18.0	17.0	.....	9.4	9.6	9.6	9.6	.....	7.6
May 14	22.1	21.5	20.0	.....	10.3	10.4	10.2	10.2	.....	8.0
May 15	.....	22.6	.....	.....	11.5	.....	10.5	.....	.....	8.0
Average daily increase	2.42	2.02	2.06	1.03	1.02	.67	.61	.65	.42	.38

no careful description has been given of natal down. This down, in the case of the Larks, is unusually heavy and so serves as a protection against the sun from which they are rarely shielded and of a color that has remarkable concealing value. The color of the down is cream-buff (from Ridgway's, 1912, "Color Standards and Nomenclature") and is distributed in the following tracts: a double patch (i. e. one on either side), on the crown, a double tuft on the occiput, a strip along the

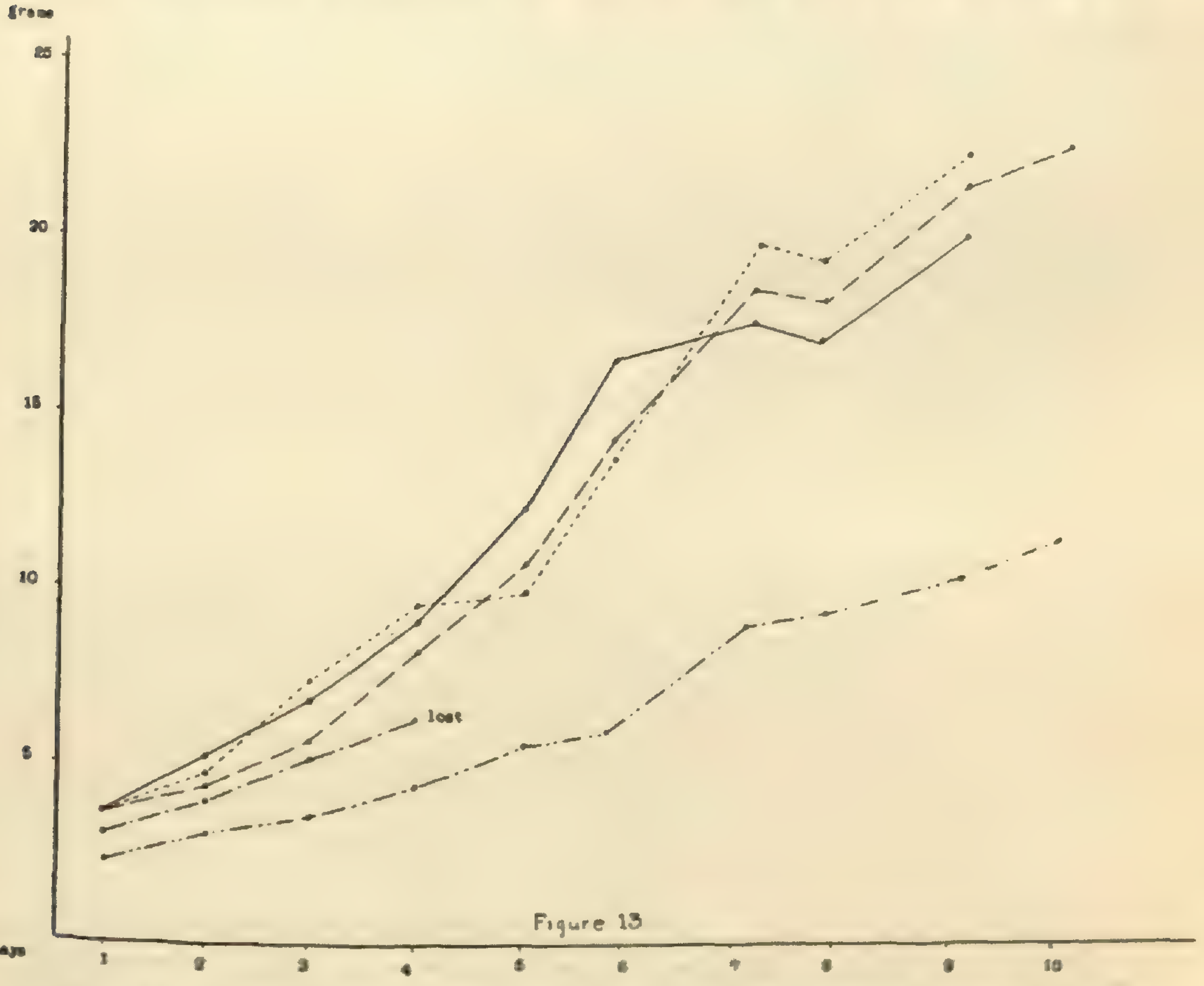


Figure 13

Fig. 13. Growth in weight of a May set of Prairie Horned Lark nestlings (nest C_1, May 6 to 15, inclusive, Ithaca, N. Y., 1927).

humerus, a strip along the arm, at the tips of the greater coverts of the secondaries, a strip on either side of the spinal column from below the wings to the tail, and, lastly, a femoral tuft.

The development of feathers depends entirely upon growth in weight, that is, upon amount of food. The descriptions here will be of a normal or optimum development. On the third day pterylae were mapped out on the side of the breast and abdomen, in small close-set whitish dots. Pterylae in fine quill tips

appeared on back, wings and head, fourth day. On the fifth day primary quills were 1.5 mm. long; breast quills .7 mm. long. On the sixth day primaries were 7.5 mm. long; feathers of the head, back and breast began to unsheath. Down began to shed on the seventh day, when primaries were 1.2 cm. long and unsheathing at the tip. Down was rapidly disappearing on the eighth day; the tail feathers protruded .15 cm. beyond the end of the body; longest primaries were 1.6 cm. long and unsheathed

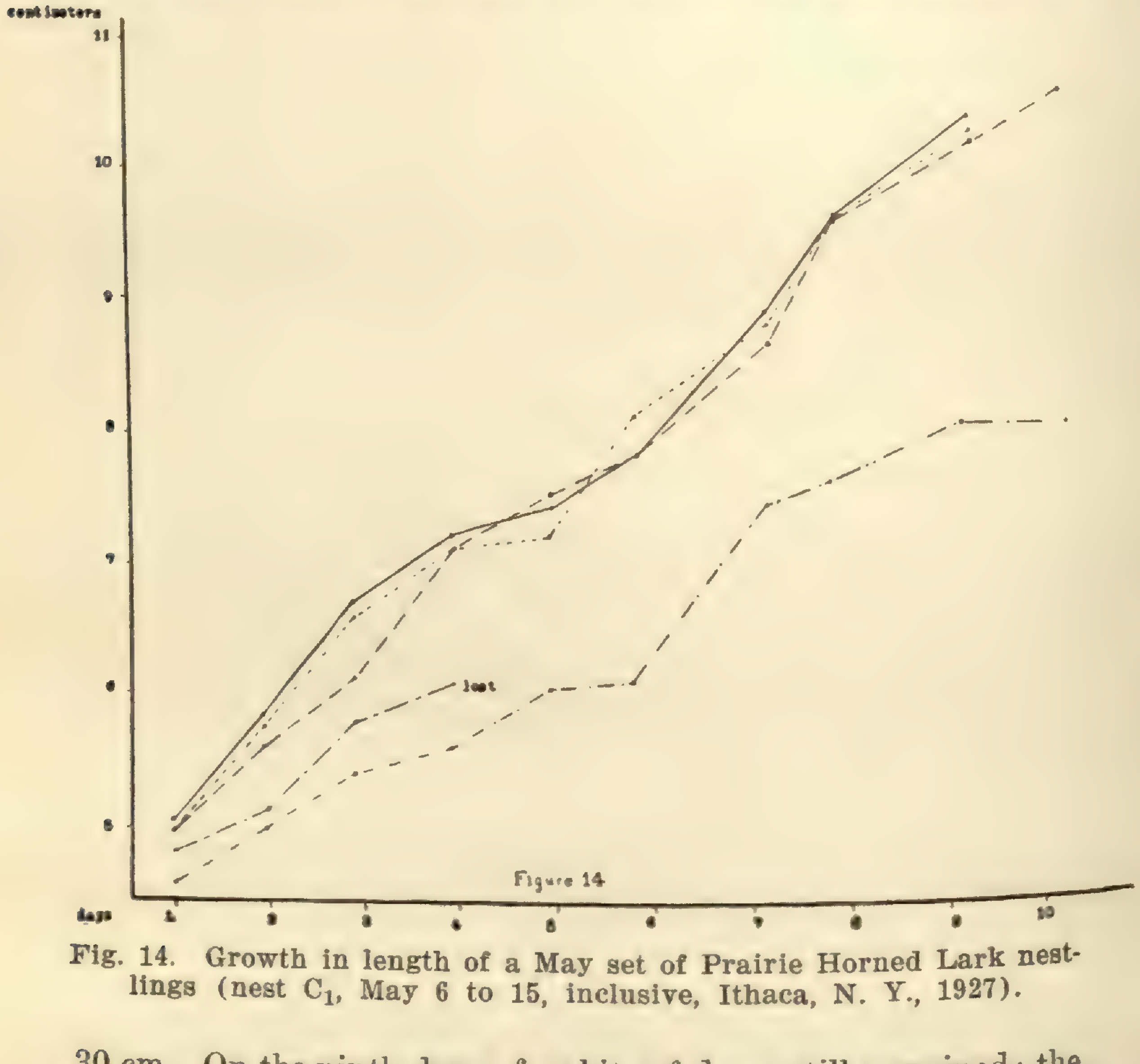


Figure 14

Fig. 14. Growth in length of a May set of Prairie Horned Lark nestlings (nest C_1, May 6 to 15, inclusive, Ithaca, N. Y., 1927).

.30 cm. On the ninth day a few bits of down still remained; the longest primary was 2.4 cm. and unsheathed .8 cm.; tail was .64 cm. On the tenth day the longest primary was 2.88 cm., open .9 cm.; the tail was 1.12 cm. long. The plumage was now essentially that of the matured juvenile: down practically off, plumage of upper surface black, each feather with a curious triangle of brown at its tip. The lower surface was white except the throat. A fifteen-day-old Lark, captured by strenuous run-

ning, presented an appearance no different from this except in size (Plate XXX).

Enemies.—Tables of mortality have been prepared which give, as far as known, the enemies of nestling Larks as well as percentages of loss by season (Tables 22, 23, 24 and Figure 11). Enemies early in the season are meteorlogical plus a scanty food supply and uneven feeding. Criddle (1920) maintains that early nests in Manitoba rarely raise more than one nestling. This is in essential accord with the writer's observations at Evanston and at Ithaca. Later enemies are predacious animals chiefly and these apparently beset the nestling after heavy vegetation has encroached upon the nestling site and so has given the

TABLE 20

Growth of a June Prairie Horned Lark nestling and its Cowbird nest-mate, to nest leaving, Evanston, Ill., 1926.

	Weight (in grams)		Length (in centimeters)	
	Lark (hatched June 8)	Cowbird	Lark	Cowbird
June 9.....	4.1	2.3		
June 10.....	6.3	4.5	5.5	5.1
June 11.....	10.0	6.6	6.2	5.8
June 12.....	13.3	9.4	7.0	6.3
June 13.....	16.6	12.6	7.4	7.1
June 14.....	17.0	14.0	7.6	7.2
June 15.....	17.1	15.3	8.0	7.5
June 16.....	20.3	16.8	8.8	7.6
June 17.....	21.7	18.4	9.2	8.0
Av. daily increase....	2.8	2.01	.53	.41

skulkers easy access under cover. The optimum season lies between late April and mid-May when weather is more lenient but the barren conditions still unaltered. Perhaps the predilection of the Lark for open, unobstructed nesting sites has been evolved through this protective advantage to the young.

The loss through improper feeding lies in the fact that incubation is begun so frequently before the set is complete; the last young to hatch then are at a disadvantage as regards position, for they are forced to the rear of the nest. The larger, in front,

receive the food; the younger, in the rear, starve, slowly, to death. Later, when food is abundant, there is a sufficient excess to pull the younger through. Then, too, more frequently in the later season, the set is often completed before incubation is begun.

Parasites were noted in one case only. This was a nest heavily infested with mites. The young here developed normally however.

The Cowbird and the Lark.—One case of Cowbird parasitism occurred in early June at Evanston (Plate XVII, Fig. 2;

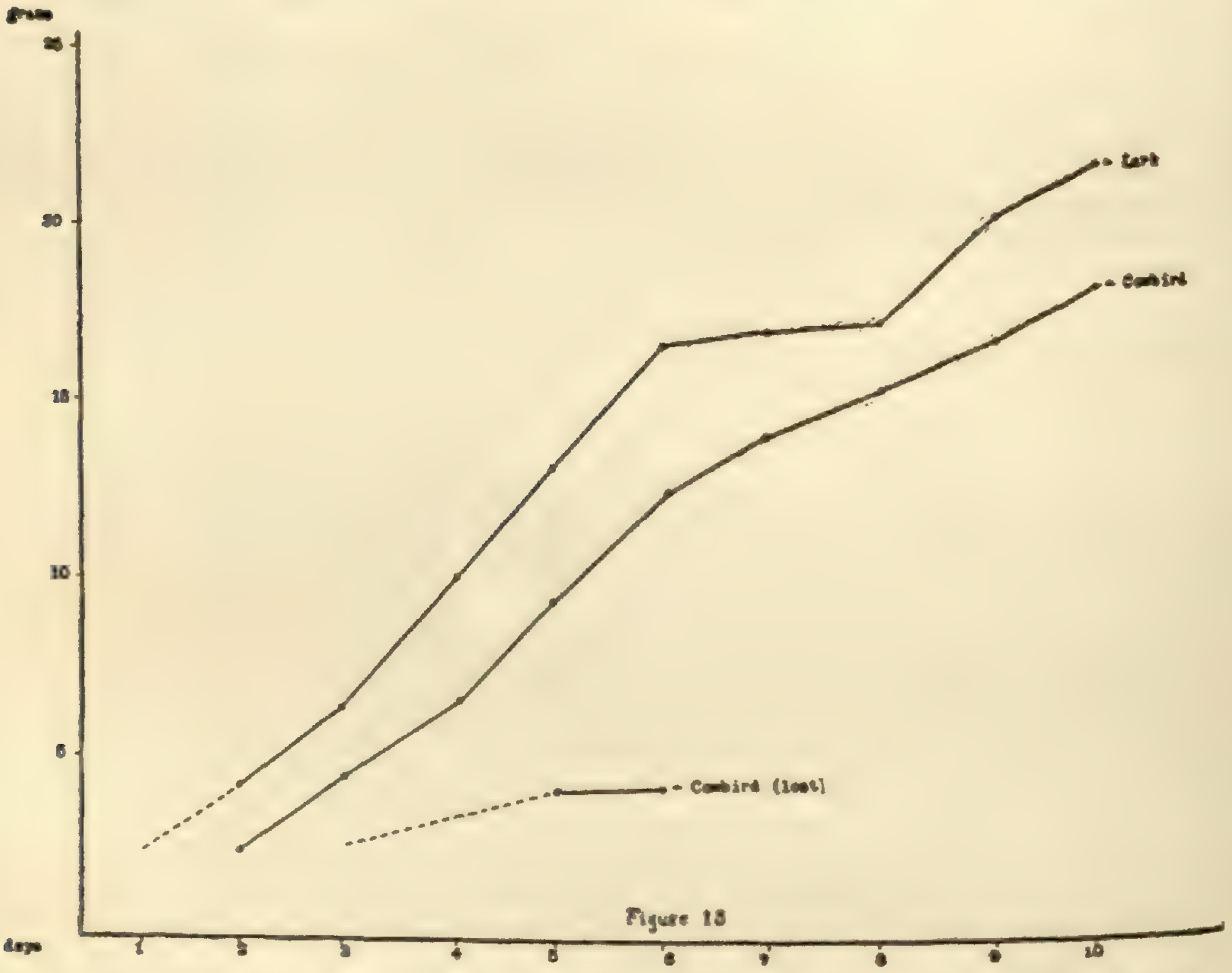


Figure 15

Fig. 15. Growth in weight of a June Prairie Horned Lark nestling and its Cowbird nestmates (nest No. 20, June 8 to 17, inclusive, Evanston, Ill., 1926).

Plate XXXII). The nest contained three Lark eggs and two Cowbird eggs. In this case one Lark hatched a day before the first Cowbird, the second Cowbird hatched on the third day and the remaining Lark eggs failed to hatch. This one-day advantage in age in the case of the Lark may explain why it developed so normally in spite of the parasitism (see Table 20 and Figure 15). But perhaps also the Lark may not be a proper host. At

TABLE 21

Daily Growth of the Prairie Horned Lark

Days Old	No. Weighed	No. Broods	Min. Weight	Max. Weight	Average Weight	Average Increase	No. Measured	No. Broods	Min. Total Length	Max. Total Length	Average Total Length	Average Increase	Average Length Tail	Average Length Longest Primary	Average Length unsheathed Primary
1	19	5	2.3	3.8	3.21	.....	10	3	4.0	5.0	4.55	.....	.....	.....	.....
2	20	6	2.6	5.9	4.57	1.36	11	3	4.7	5.8	5.20	.65	.....	.....	.....
3	18	6	3.6	8.6	6.36	1.79	15	5	5.5	6.7	5.96	.76	.....	.....	.....
4	13	5	4.7	10.0	8.30	1.94	11	4	5.6	7.2	6.38	.42	.....	.....	.....
5	10	5	5.8	13.6	10.66	2.36	9	4	6.1	7.5	6.91	.53	.....	.20	.....
6	7	3	6.0	16.6	12.48	1.82	7	3	6.1	8.1	7.34	.43	.....	.70	.....
7	6	3	9.0	19.9	15.58	3.10	7	3	7.2	8.9	8.02	.68	.10	.15	.30
8	6	3	9.4	19.2	15.65	.07	7	3	7.6	9.6	8.61	.59	.27	1.50	.43
9	6	3	10.3	22.1	18.06	2.41	7	3	8.0	10.3	9.32	.71	.63	2.30	.66
10	4	3	11.5	22.6	18.02	.....	4	3	8.0	10.5	9.30	.....	.83	2.50	.86
11	2	2	17.0	22.0	18.50	.....	1	1	.....	.....	10.60	.....	1.11	3.49	1.74
12	1	1	.....	.....	18.10	.....	0	.....	.....	.....	.....	.....	.....	.....	.....
15	0	.....	.....	.....	.....	.....	1	1	.....	.....	12.00	.....	2.50	5.40	.....

Weight in grams; length in centimeters.

the end of ten days the Lark left the nest normally, but the Cowbird was still far behind the Lark in development. The following day the nest was empty and the ultimate fate of the Cowbird is not known. Space does not permit an extensive speculation as to why the Prairie Horned Lark is not more frequently parasitized but a few points may be noted:

1. The Lark is not as small as the usual host and there was but little discrepancy in egg weights (Cowbird 3.12, Lark 2.65 grams).

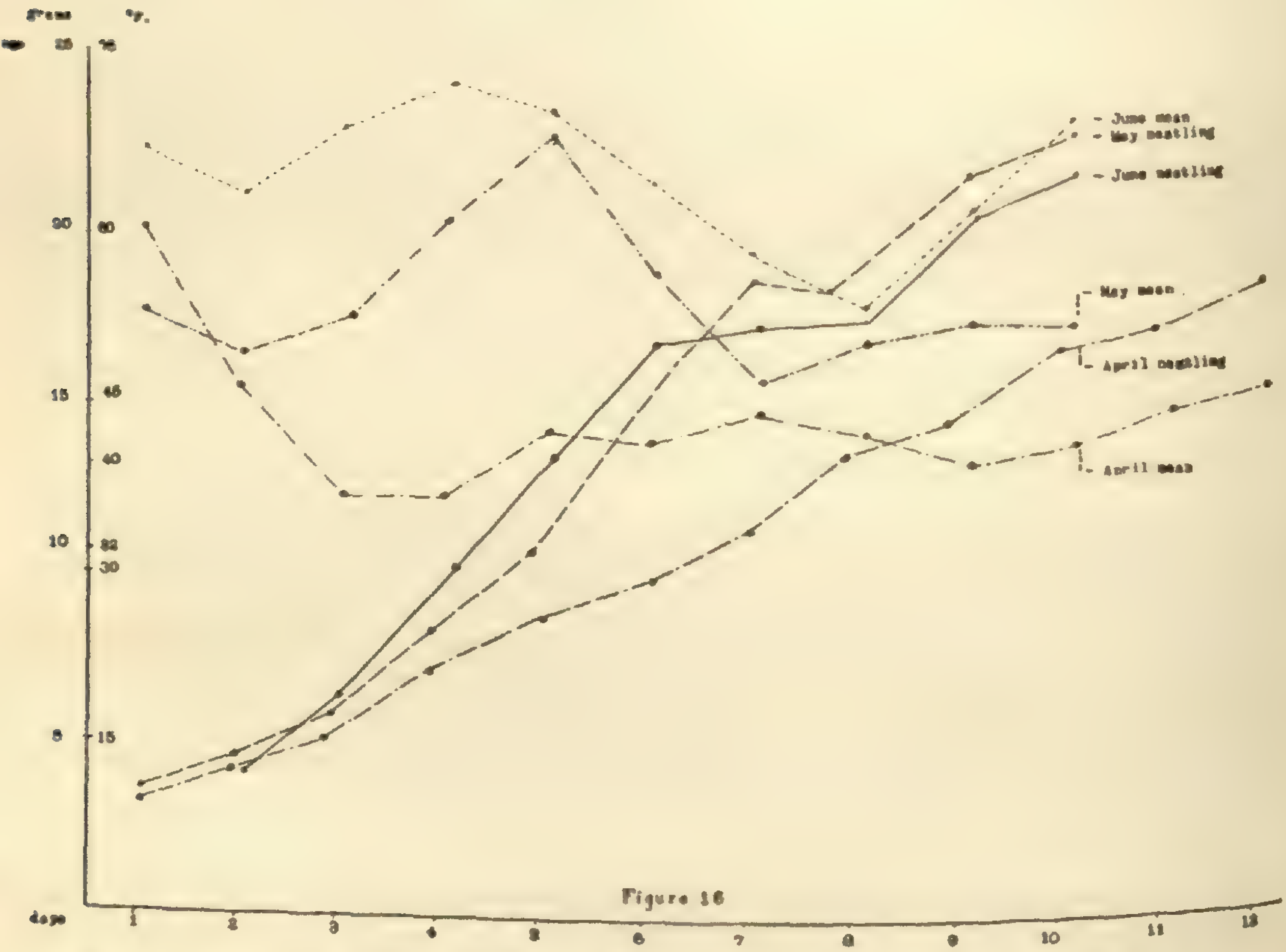


Fig. 16. Comparative curves of growth of an April, a May and a June Prairie Horned Lark nestlings with curves of the mean daily temperatures of the same periods (nests B_2, April 21 to May 2, inclusive, Ithaca; C_1, May 6 to 15, inclusive, Ithaca; and No. 20, June 8 to 17, inclusive, Evanston).

2. Fully half of the nesting season of the Lark is prior to sexual maturity of the Cowbird in the spring.

3. The incubation period may not be such as to favor parasitism.

4. The exposed condition of the nest may be detrimental to the scantily downed Cowbird.

5. In the case noted the Lark eggs (or at least egg) was laid before the Cowbird, apparently, and incubation may have begun then.

6. The food, in June at least, is favorable, however. At Ithaca I placed a newly hatched Cowbird in a nest with Lark eggs. The Cowbird prospered and when removed ten days later was well developed and weighed 21.7 grams, about the weight of a Lark at that age. However, young Larks would have gone from the nest at this age but the Cowbird was not yet ready to do so.

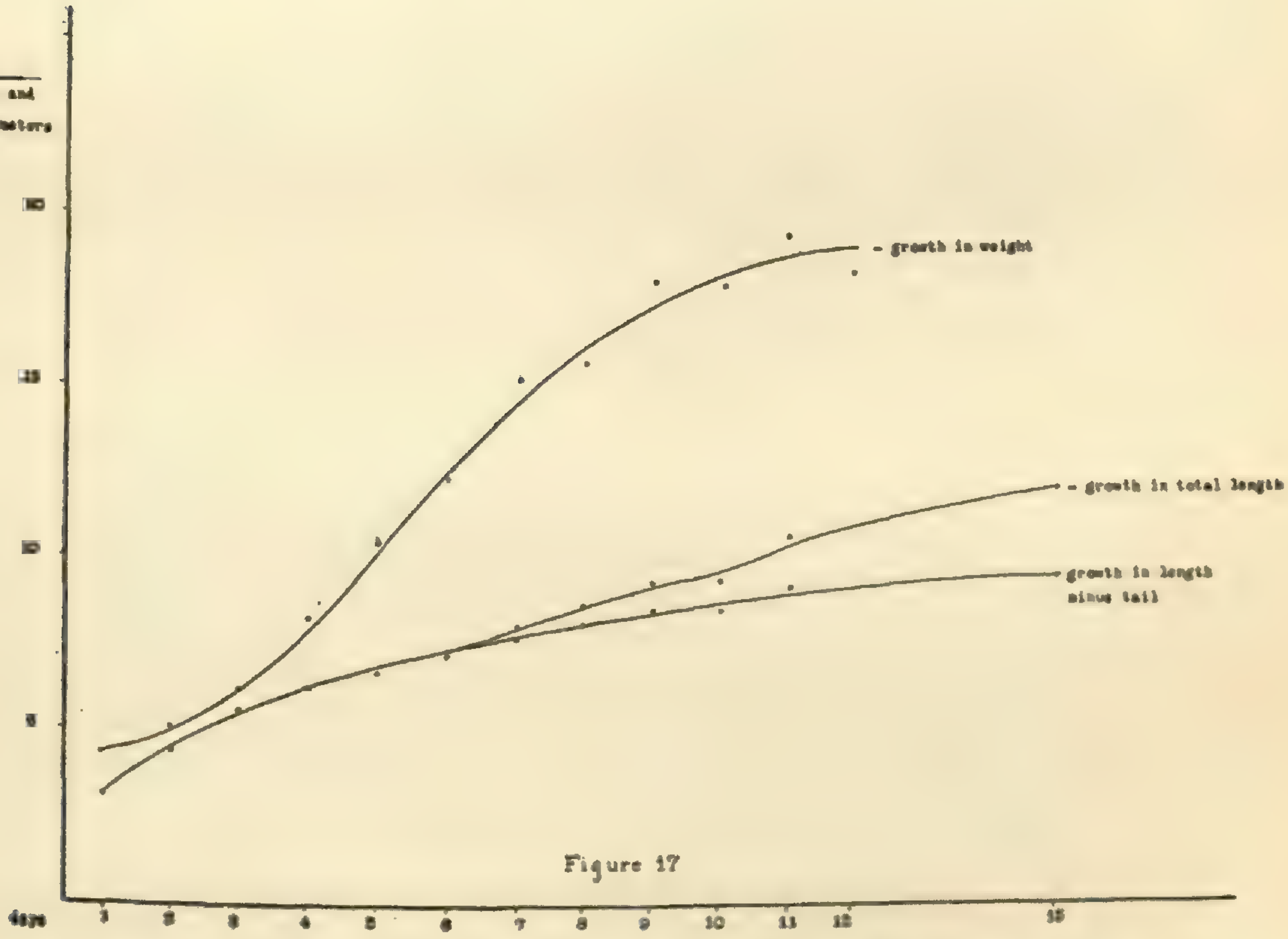


Figure 17

Fig. 17. Average growth in weight and length of a varying number of Prairie Horned Lark young.

7. The Horned Lark has no aversion to foreign eggs for a Song Sparrow egg, placed with Lark eggs, was not disturbed.

Here, then, seems to be a possible host that for reasons not quite clear the Cowbird almost wholly overlooks.

Protection for the young.—As birds of the open, and on the ground, the young of the Larks have need for two important features to protect them: silence, and the proper coloration. These two characteristics they possess in remarkable degree. At

TABLE 22

Mortality table of nestings of the Prairie Horned Lark for 1926 at Evanston, Ill.

Nest No.	Inclusive Dates*	No. of Eggs	Egg Loss	Cause	No. of Nestlings	Nestling Loss	Cause	Successful Nestlings
1	March 22-25	2	2	Snow	0			0
2	March 22-25	2	2	Snow	0			0
3	April 11—May 1	4	1	Failure to hatch	3	2	Disease 1 Starvation 1	1
4	April 12—May 3	4	0		4	0		4
5	April 12—May 4	4	0		4	0		4
6	April 12—April 27	3	0		3	3	Unknown	0
7	April 13—May 5	4	0		4	2	Starvation	2
8	April 13—April 20	3	3	Unknown	0			0
9	April 13—May 7	3	1	Unknown	2	0		2
10	April 13—May 9	4	0		4	1	Starvation	3
11	April 14—May 5	3	1	Failure to hatch	2	1	Unknown	1
12	April 14—May 5	3	0		3	0		3
13	April 26—May 20	5	0		5	0		5
14	April 27—May 19	4	0		4	1	Starvation	3
15	May 3—May 24	3	0		3	1	Disease	2
16	May 7—May 9	3	3	Unknown	0			0
17	May 9—June 2	2	0		2	0		2
18	May 21—June 12	3	0		3	0		3
19	May 22—June 7	5	0		5	5	Unknown	0
20	May 25—June 17	3	2	Failure to hatch	1	0		1
21	June 9—June 26	5	1	Failure to hatch	4	4	Weasel?	0
22	June 17—July 11	4	0		4	1	Unknown	3
23	June 22—July 5	2	1	Failure to hatch	1	1	Unknown	0
24	June 27—July 12	4	1	Failure to hatch	3	3	Unknown	0
Total		**82**	**17**		**65**	**26**		**39**

*The first date in each case indicates date first egg is laid, this date is estimated.

Summary: Per cent of loss in eggs: 20.7
Per cent of nestling loss in total number of nestlings: 40
Per cent of loss of whole after hatching: 31.7
Per cent total loss of 82 eggs: 52.4

TABLE 23

Mortality table by months of nestings of the Prairie Horned Lark at Evanston, Ill., 1926

Month	No. of Eggs Within the Month	Egg Loss	Per Cent of Egg Loss	No. of Nestlings Within the Month	Nestling Loss	Per Cent of Nestling Loss	Total No. Eggs and Nestlings	Total Loss Eggs and Nestlings	Per Cent Total Loss
March	4	4	1.000	0	0	.0	4	4	1.000
April	44	9	.204	30	6	.200	74	15	.202
May	28	3	.107	23	6	.260	51	9	.176
June	26	3	.115	20	9	.450	46	12	.260
July	6	2	.333	8	5	.625	14	7	.500

TABLE 24

Mortality table of nestings of the Prairie Horned Lark for 1927 at Ithaca, N. Y.

Nest No.	Inclusive Dates*	No. of Eggs	Egg Loss	Cause	No. of Nestlings	Nestling Loss	Cause	Successful Nestlings
B_1	March 15—31	3	0		3	3	Low temperature	0
A_1	March 19—April 1	2	2	Snow	0			0
B_2	April 8—May 2	4	0		4	3	Low temperature	1
D	April 8—April 19	3	3	Cultivation				0
C	April 21—May 15	5	0		5	2	Unknown 1, Expos. 1	3
A_2	April 22—May 16	3	0		3	0		3
Total		20	5		15	8		7

*First date in each case is estimated.

no time does the young Lark have an audible food call (such as the continual clamor of young Cowbirds or young Baltimore Orioles, for instance), except when the parents are directly at the nest. Even then it is not audible more than a few feet away. In all plumages the young are remarkably concealed whether it be their clay-colored down or their mottled juvenile plumage, which is such a remarkable "picture pattern" of the lights and shadows about a ground nest (Plate XXXIII).

The actions of the parents, especially abandonment concealment and a stern reluctance to approach a nest in which there are young, are well calculated to protect ground nests.

Nest leaving.—The age of the young at nest-leaving depends upon the manner and amount of food they have received. The average is between the tenth and eleventh day. Some go on the ninth, one set remained until the fourteenth. They go, usually, merely by following a parent who has just brought them food. In one case I observed the female entice a belated youngster from the nest by coming up with food and retreating until his hunger forced him out.

Just prior to nest leaving, as has been noted, the young acquire a "crouch-concealment" habit that stands them in good stead once they are away from the nest. This crouch or "freeze" is maintained at all times, when the parents are not near, up to five or six days after nest-leaving (Plate XXXIV). If they are disturbed when in this "crouch-concealment" they will not return to it unless left for a moment with one of the parents. This habit, plus their peculiar plumage, makes the Lark similar to the precocial young of a gallinaceous bird as Chapman (1918) has noted. Indeed the Larks are semiprecocial in many respects, not the least of which is the habit of leaving the nest several days before they can fly.

Many writers have noted that the young Larks leave the nest before they can fly and Forbush (1911) sets this time at a week. This is a little too long however. By banding the young I was able to get some definite material on this. Thus one young was caught, able to make flights of about one hundred yards, at fifteen days of age. This one had been out of the nest just five days.

The parents must find their quiet youngsters, in their crouch-concealment, by some method other than sound. To do this

they hover in a peculiar fashion here and there until the crouching Lark is seen.

One other matter of interest with regard to recent nestlings remains to be noted. That is that the young hop, do not walk. Apparently Brooks (1908), is the only other writer who has noticed this. It may be a recapitulatory feature harking back to a hopping ancestor or, more likely, it is merely an anatomical defect in the young which has no ancestral relationship. In any case walking is not learned for several days and when first attempted is a slow waddle with legs spread widely. Rapid locomotion for many days is accomplished by hopping. One of my most trenchant recollections of the Larks is of a female moving rapidly off down an old wheel rut and running, with a young Lark following and going just as rapidly as she—but hopping.

MOLT.

Activities subsequent to nesting have been taken up in a general way under fall and winter activities. A word or two remains to be said of molt. Dwight (1890) was, it seems, the first to show that the transition from the juvenile plumage to the adult is accomplished by a complete molt of wings and tail as well as body feathers. This molt, in the case of *praticola* occurs between late July and late August. Dwight also brought out the fact that there is but one molt in the year for adults too, the post-nuptual. Breeding plumage comes about by the wearing off in late winter of the brown tips that obscure the black areas of crown, cheek and throat.

ECOLOGY OF THE NESTING-SITE OF THE PRAIRIE HORNED LARK IN RELATION TO OTHER BREEDING BIRDS AT EVANSTON, ILL.

At Ithaca, N. Y., because of the comparative uniformity of the conditions of the breeding area, there was not presented the opportunity, as at Evanston, Ill., of observing a large number of other breeding birds near at hand. As a matter of fact the situation at Evanston was unique in that the subdivided golf course with its torn street-ways, old hazards, grass and meadow areas and weed patches, all allowed now to proceed uninter-

ruptedly, produced a veritable gamut of ecological conditions during spring and summer which proved suitable to a long series of birds. Since the flora, here otherwise undisturbed, was modified with the advance of season, it follows that the ecological categories of the open field were modified likewise and were followed, as a consequence, by a change of population wherein the Prairie Horned Lark figured conspicuously.

Because opportunity was presented thus so ideally to make close comparisons between Lark and its open field congeners, this treatise will not be complete without so comparing. The Lark began to nest in March with flora at its minimum and suitable breeding territory extensive, and continued to nest into July when flora was at its maximum and suitable areas greatly reduced. Such a change closed some territories completely and greatly modified others. But what was unsuitable for Larks proved highly acceptable to others and it is this succession that interests us here. This succession was both seasonal and, in June, geographical. For instance, a region might satisfy, with its seasonal conditions, the Lark in March and April, the Vesper Sparrow in May and the Dicksissal in June. Such conditions were frequently presented at Evanston. Likewise, at a single period in June, the same sequence would be presented by walking from an old sanded hazard to a neighboring weed patch.

In addition to ecology of habitat the dates of arrival, seasons of song and other characteristics of interest are given and reference made back in each case to the Prairie Horned Lark, our main thesis. This material can be presented best by considering the species separately.

Bartramia longicauda. Upland Plover. Notes of this bird were heard on the main subdivision June 17, 1925. In 1926 they were first heard in April 21, and almost daily thereafter until May 8, when a peculiar interval occurred with no records. They were noted again on May 30 and with one or two exceptions were seen or heard daily until July 22, the last visit to the area.

On April 26 that most astounding weird and mournful wail (song), of the Plover was first heard and frequently from that time to July 12.

On June 18 a nest with three eggs was found in the timothy

just northeast of the Main Subdivision. One of these eggs hatched July 4, the other two, though fertile, failed to hatch.

Extensive data were collected concerning calls, song and breeding reactions but space does not permit their inclusion here. There were two or three pairs of these interesting birds in the vicinity and it is possible that one pair may have nested on the Main Subdivision. The musical calls of these birds together with their uncanny song provided an atmosphere well in keeping with the open areas where the Prairie Horned Lark was also at home. The nesting habitat was that of comparatively tall, close-set, uniform timothy.

Actitis macularia. Spotted Sandpiper. Arrived April 30, 1926, but did not appear on the subdivision until May 22. A puddle there then, formed by late May rains, proved an attraction for several days. A pair nested in block No. 19 not ten feet from the sparrow trap that I visited daily. The nest was found June 6 (first day of incubation, I believe), the eggs hatched June 25: an incubation period of twenty days. These young, with their parent, remained on or near the subdivision until July 17.

The nesting habitat was in sparse but coarse weeds such as evening primrose *(Oenothera biennis)*, white sweet clover *(Melilotus alba)*, Mare's tail *(Hippuris vulgaris)*, wild lettuce *(Lactuca sp.)* and squirrel tail grass or wild barley *(Hordeum jubatum)*.

Oxyechus vociferous vociferous. Killdeer. The Killdeer came March 19 and was a conspicuous element in the bird life of the subdivision from that date to late July. Though they were there daily none actually bred on the Main Subdivision but rather seemed to use it as a feeding ground. However one nest was located on the West Subdivision, July 6; subsequently destroyed by a mower, July 15. It was located in the old vegetable garden, in an area of bare ground with sparse young weeds, such as *Chenopodium, Xanthium* and *Setaria*, beside a small plant of wild lettuce *(Lactuca canadensis)*.

Dolichonyx oryzivorus. Bobolink. Came on May 8, 1926. One was taken in my sparrow trap on May 14. On May 16 they were present in numbers and in riotous song and from that time on formed the most conspicuous living element of the subdivisions. A second was taken in the trap May 21, the first

female was seen May 22, maximum numbers seemed to be reached May 23. Not one of the daily visits from June 1 to late July failed to disclose Bobolinks, they could not be overlooked.

From the time of their arrival until the young hatched, females seem to be almost non-existant. They are as seclusive as their males are obvious. Nests with eggs are almost impossible to find for the brooding birds either do not flush from them under any circumstances or slip off through the dense grass at the approach of the searcher. Rope dragging over most of the Main Subdivision in June, did not locate a nest definitely.

The female comes to the weed tops with the hatching of her young and her sharp "chink, chink" is sign of a nest near. By observing a female with food one nest was located June 18 (not on subdivision) with three eggs and three newly hatched young. Another (on the Main Subdivision) was found on July 17 with young near nest-leaving age.

The great fervor of song from the males begins to abate after the first week of July and gradually the quieted adults and young disappear from the breeding ground. In 1926, the breeding birds were reduced to two or three pairs, by July 9, and from then on there were fewer songs than formerly. Even these few songs were still further reduced on subsequent July visits until on July 21 the last birds noted were adults carrying food to belated nestlings, quiet now except for scolding notes. On July 29, 1925, large flocks of Bobolinks collected on the weedier parts of the subdivision (in patches of *Oenothera, Melilotus, Ambrosia* and *Cirsium)* and, though the majority of these were young birds, a goodly number of adult males were with them in various stages of molt. Their only note now was a pleasantly metallic "chink."

A census of singing males showed fourteen pairs of breeding birds on the Main Subdivision (about 90 acres), in mid-June. Each of these had a definite territory which any male would sharply delimit if he were persistently driven from place to place. One such territory was roughly rectangular, sixty by ninety yards, about the size of territory of the Lark. Yet the males, in their exuberance, frequently flew into each other's territory or, if a female appeared, might collect in threes or fours near her. In spite of this the Bobolinks were never ob-

served to fight or to drive away intruders as the Prairie Horned Lark did invariably.

The breeding season and the song of both Larks and Bobolinks ended nearly at the same time but the similarity stopped there. The Lark, nearly resident, sang from late January to early July, bred from March to mid-July, whereas the Bobolinks, highly migratory, sang from mid-May to early July, bred from late May to mid-July.

Located nests were in the densest, though not tallest, vegetation. One was at the base of a clump of young evening primrose *(Oenothera biennis)*, another in heavy plantain *(Plantago major)* blue grass *(Poa pratensis)* and wild strawberry *(Fragaria sp.)*. Thus the Bobolink is near one end of that series of ecological habitats of the open field determined by the density of vegetation—the Prairie Horned Lark at the other.

Molothrus ater ater. Cowbird. Though the Cowbird arrived on April 16, in 1926, the first did not come onto the subdivision until April 30. Thereafter the bird was a frequent member of the fauna until June 27, when the last was noted. Females, apparently nest hunting, were flushed from the grass on May 16 and May 26. In addition to the one case of parasitism of the Prairie Horned Lark (for which see back), there were also noted on the subdivisions one case of parasitism of a Vesper Sparrow (Sparrow was seen feeding young Cowbird) and another of a Song Sparrow (male was seen feeding the young Cowbird).

Sturnella magna magna. Meadowlark. Next to the Bobolinks, the Meadowlarks claimed the eye and ear of the observer upon the subdivisions. In the fall of 1925 they were seen on October 4, 25 and 31. Those observed on October 4 had congregated in the marsh just south of the subdivision and were maintaining a remarkable jargon of experimental song—none full, but snatches of the real thing and all birds doing it at once.

In 1926, the first returned March 19 and at the time of the great snows of late March many birds were on the barren subdivisions. On April 1, I waded the more than a foot-deep snow to find that the Prairie Horned Larks were off their territories, off the subdivisions and along the roadside and the Meadowlarks

were sitting in sunny pockets of the snow about the cornstalks of the West Subdivision—and there singing.

Meadowlarks were observed every day from early April to late July. The maximum number seemed to be reached by April 28. Three nests were located, one only on the subdivisions. A nest of June 11 had three eggs, a nest of June 20 had five eggs which hatched June 25, young left the nest July 4 and 5 at an age identical to the nest leaving of most of the Prairie Horned Lark nestlings. A nest of July 18 had two young, well-fledged, near nest-leaving. On June 23, and subsequently, family groups were in evidence. A mid-June census showed seventeen pairs on the Main Subdivision.

By the first week of July songs were fewer and less vigorous but were still given occasionally even to the end of the month.

The breeding habitat of the Meadowlark is that of comparatively low but heavy grasses. Nests seldom occur in dense leafy growths of dicotyledonous herbs as do those of the Bobolink and Dicksissel. The one located subdivision nest was in a broad expanse of blue grass *(Poa pratensis)*. Thus the Meadowlark, in the relationship of its breeding habitat to vegetation comes somewhat between the Dicksissel and Bobolink at one extreme and the Prairie Horned Lark at the other.

Pooecetes gramineus gramineus. Vesper Sparrow. On April 16, 1926, the first definite songs of the Vesper Sparrow occurred on the subdivisions. The day following they were numerous, and every day from that date until late July they are recorded in my notes.

The Vesper Sparrow remained in full song later than any other resident of the area and even on July 21, with nearly all other bird voices hushed, his voice still rang out across weed and grass tops of the West Subdivision. In broad day and full sun the Vesper Sparrow sang in May and June but evening and cloudy days found him at his best and fullest. In July the song was restricted nearly entirely to the evening.

One nest was located on the Main Subdivision June 8. It contained four eggs of which one hatched July 18, two others July 19, and one failed to hatch. The young left the nest June 28 with one at the eleventh day and two at the tenth. The June census showed five pairs of nesting birds on the Main Subdivision, nearly all in old hazards.

Of all resident birds of the subdivisions the Vesper Sparrow is nearest the Prairie Horned Lark ecologically. The above nest was in an old hazard depression of bare ground chiefly, with scattered tufts of squirrel tail grass *(Hordeum jubatum)*, and red top grass *(Agrostis palustris)*, the only verdure. The nest itself was built partially under a little pile of old dead and dried weed stems. The Vesper Sparrow thus occupies the sparse weedy regions, regions with trash and much bare ground, the nearest approach to the nearly bare open where the Prairie Horned Lark nests are found. Thus in the series the Vesper Sparrow comes in the second ecological breeding niche that starts with the Prairie Horned Lark in the barest of habitats and reaches to the Dicksissel in the densest. Another viewpoint is of great interest in this connection, in that the locations of the ecological niche for both of these birds varied with the season. By late June the last breeding areas of the Main Subdivision had, with the press of summer verdure, become inhospitable to the Lark and the birds that were still breeding were in the more suitable ground of the West Subdivision. For a while longer the Vesper Sparrow remained in the Main Subdivision but July found it following the Lark—two weeks of plant growth behind the former.

Passerculus sandwichensis savanna. Savannah Sparrow. My notes contain a record of this sparrow on October 25, 1925. The first definite record for 1926 is April 16, when two were taken in the ground trap on the Main Subdivision The first songs were heard April 22. Others were taken in the trap May 3, 6, 9, 13, 26. This little sparrow was numerous in the area throughout the entire season and was noted daily until July 21 (the last regular visit to the region). Songs were frequent until June 18, when there was a noticeable letting off probably coincident with the hatching of the young. However, singing was maintained until the middle of July. The census of mid-June showed nine breeding pairs.

No nests were located in Evanston in spite of the large number of breeding birds but the birds preferred the tall heavy quack grass *(Agropyron repens)* and, later, the red-top grass *(Agrostis palustris)*. A nest, located at Ithaca, New York, was in tall grass of mixed *Agropyron repens* and *Dactylis glomerata* (orchard grass) so dense that long searching was necessary to find it even though the bird flushed at my very feet.

If the Ithaca nest is indicative of the ecological habitat then the Savannah Sparrow is fourth in the series from the Prairie Horned Lark to the Dicksissel, from the bird breeding in the scantiest vegetation to the bird of the heaviest: (1) Prairie Horned Lark, (2) Vesper Sparrow, (3) Meadowlark, (4) Savannah Sparrow, (5) the Bobolink, (6) Dicksissel.

Ammodramus savannarum australis. Grasshopper Sparrow. A single individual sang on the Main Subdivision April 28, 1926; none from that date to May 8; none again until June 1, but the Sparrow was noted regularly from this last date until the maximum number of singing males seemed to be reached on June 13. From that date to July 21 they were noted daily and in song. The mid-June census showed twelve breeding pairs on the Main Subdivision.

It may be of interest to note here that these birds have two distinct songs: (1) the "click-ik, z-z-z-z-e-e-e-e-" described by most writers and (2) a "click-ik, zeah, uhah, zeah, uhah, zeah, uhah," or "click-ik, z-z-z-zwea, z-z-z-zwea, z-z-z-zwea," buzzing and insect-like as the first but interrupted and undulating, totally distinct from the song ordinarily described. To say "life's a rigmarole, rigmarole, rigmarole" with all the buzz at one's command gives a good notion of the quality of the song. It seemed to be given more frequently in the evening, the first more frequently during the middle of the day. That it is not a peculiarity of northern Illinois Grasshopper Sparrows is shown by the fact that an Ithaca, New York, bird knew it also.

Since no nests were located the ecological habitat cannot be definitely assigned. But the birds were found in conditions similar to those occupied by the Savannah Sparrow, viz., tall and heavy grasses such as *Agropyron repens* and *Agrostis palustris.*

Spiza americana. Dicksissel. This, the last resident to arrive on the subdivision, was noted first May 29, 1926. The first songs were noted May 31, and from that time to the last of July its presence could not be overlooked. The maximum number of singing males was reached June 10. No definite effort was made to locate nests but the birds persisted in the taller, ranker growth of the area, especially wherever white sweet clover *(Melilotus alba),* the canada thistle *(Cirsium arvense)* and wild lettuce *(Lactuca sp.)* abounded. The Dicksissel will nest in meadows

of clover, alfalfa or timothy but here they avoided the larger areas of blue grass, red-top grass, quack grass and timothy, restricting themselves to much coarser vegetation. This is in accord, too, with frequent observations I have made of them in eastern Nebraska, where scores of nests have been seen. Nine breeding pairs were shown by the June census, nearly all in such conditions as described.

If, in a large area such as these subdivisions, where every pos-

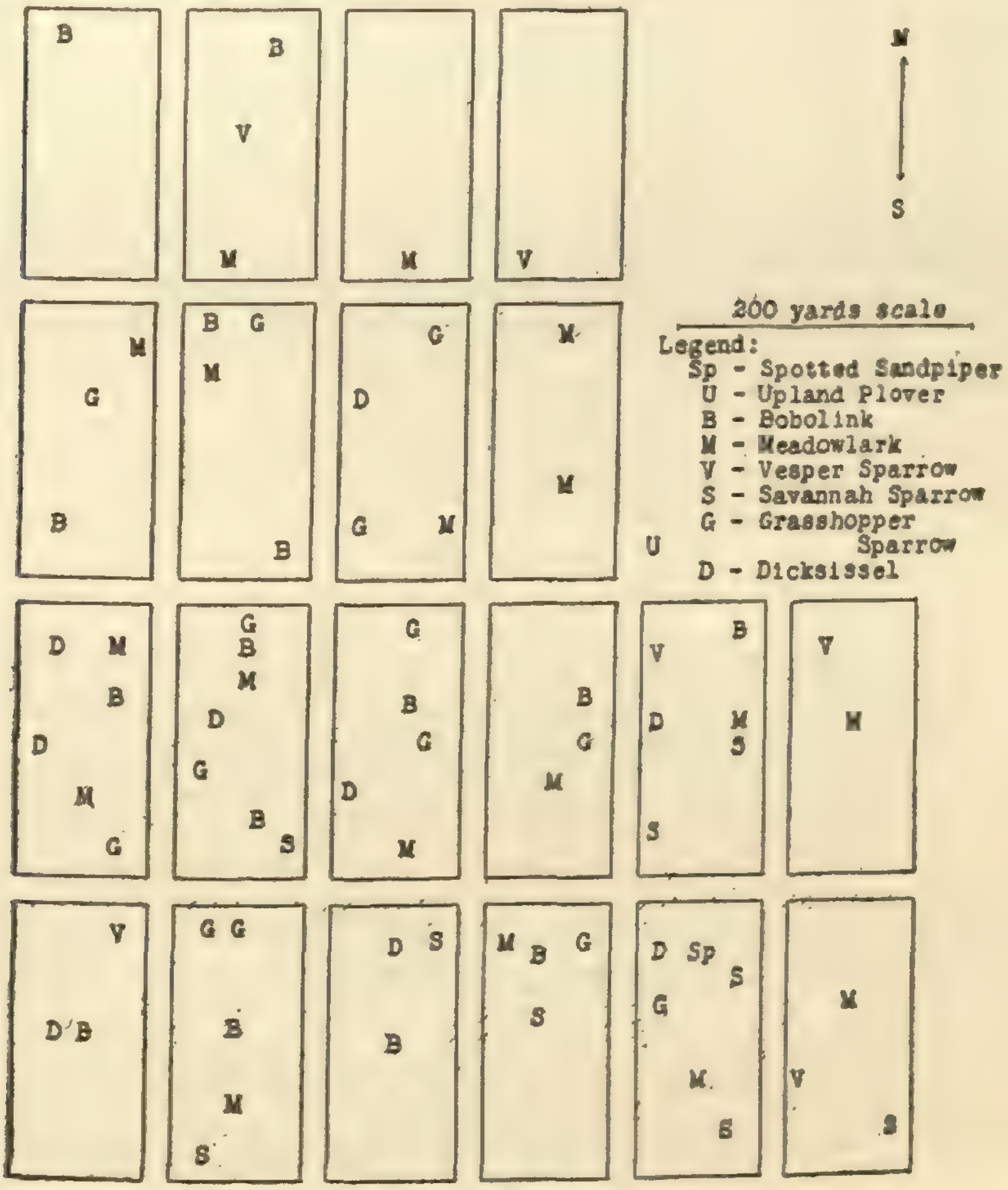


Fig. 18. A June census of the breeding birds, other than the Prairie Horned Lark, of the Main Subdivision at Evanston, Ill., 1926, with the approximate location of the nests.

sible habitat of the open field prevailed, the Dicksissel chooses the heaviest growth of large herbs, then such preference places him sixth in the ecological categories that vegetation erects: the Prairie Horned Lark in the scantiest growths, then the Vesper Sparrow, then the Meadowlark, then the Savannah Sparrow, then the Bobolink, and, lastly, the Dicksissel.

Summary of all breeding birds of the region in June:

Spotted Sandpiper	1
Upland Plover	1
Prairie Horned Lark	4
Bobolink	15
Meadowlark	18
Vesper Sparrow	5
Savannah Sparrow	9
Grasshopper Sparrow	12
Dicksissel	9
Total number pairs	74
Largest number in one block	7
Smallest number in one block	1

NON-BREEDING BIRDS THAT FED ON OR ABOVE THE TERRITORY OCCUPIED BY THE PRAIRIE HORNED LARK AT EVANSTON, ILL.

Though not so significant as breeding forms of the region still a final item of some interest is that which completes the remaining avifauna found in the vicinity of the home of the Prairie Horned Lark. The open field did not present a suitable breeding ground for these or was not in the proper latitude, yet on it or above it they appeared and because of this they have a relationship to our main subject.

Grus mexicana. Sandhill Crane. Two alighted on the West Subdivision, May 2, probably attracted there by the ungathered corn.

Phasianus torquatus. Ring-necked Pheasant. The Pheasant was heard crowing throughout the spring in the grassy marsh to the south and a pair was flushed from a weedy hazard in July, 1926.

Zenaidura macroura carolinensis. Mourning dove. The Main Subdivision and that to the west were favorite feeding areas for the Dove. Here the bird was noted first July 4, 1925, again October 4 and 25, 1925. In 1926 the first was seen March 19, but none again until April 18. From this latter date until July 22 (the last visit) they were noted daily, occasionally two or three only, but again in flocks of ten to twenty.

Love flights were frequent and songs occasional though the subdivisions were not breeding grounds but a mutual feeding place. On the Main Subdivision the Doves were always in the old sand hazards, very probably securing grit, but on the West

Subdivision a small field of ungathered corn provided an endless resource of soft, rain-soaked and sprouting food. Here, in July, hundreds gathered, and a journey across the field would be accompanied by intermittent, sharp staccatos of wing whistlings as flock after flock arose. The Mourning Dove is not a common breeding bird in Northern Illinois, indeed, not a single nest was located in four years in the vicinity of Evanston. It is probable then that these birds, so numerous here, were coming from breeding grounds many miles away and from many diverse localities, to these unusually prolific feeding areas, since they appeared in small flocks through the spring and summer. The fact that no young birds were noted, even in July, further enforces the viewpoint of their distant journeys.

Circus hudsonius. Marsh Hawk. The subdivisions were hunting grounds for the Marsh Hawks, but they did not breed there though possibly they did so in the weedy marsh to the south. This hawk was noted first on March 19, 1926, and regularly, though not daily, from that time until May 2.

Falco sparverius sparverius. Sparrow Hawk. This little falcon nestled in a woodland northwest of the subdivisions and hunted over this area almost daily. Perhaps it may be held accountable for some of the destruction of nestling Larks. The hawk was seen November 25, 28, 1925, January 28, February 7 and 28, 1926, and very frequently from that time on during my visits to the area.

The adult Larks showed no fear of the Sparrow Hawk, but when once it alighted near a Lark nest the birds ceased feeding their young for a period of more than thirty minutes during its stay and complained vociferously the while.

Asio flammeus. Short-eared Owl. Observed on the Main Subdivision, October 25, 1925. First observed in 1926 on April 16, a day of considerable migration, apparently, for three were noted. One was flushed April 29, one again April 30, and the last noted was hunting over the area, about sundown, on June 28.

It is probable that the short-eared Owl was no factor in the economy of the Lark, first because it did not breed near, apparently, and secondly because it was probably not eating birds. A few pellets examined (April 20) contained fish scales and fish bones only.

Melanerpes erythrocephalus. Red-headed Woodpecker. The

same neglected corn which proved such an attraction to Mourning Doves on the West Subdivision was also the reason for the presence of Red-headed Woodpeckers there. Throughout July these birds were noted in twos and threes on the field.

Colaptes auratus luteus. Northern Flicker. The Flicker found ants on the subdivisions and was a more or less constant member of the bird fauna there. Observed there October 4, 1925, on April 23, 1926, and more or less regularly until July 17, 1926.

Chordeiles virginianus virginianus. Nighthawk. The first flew over the area on May 21, 1926, several on May 31, and no evening's observation from that time until July 15, failed to note them.

The marshes to the south, the stagnant water of the open, newly laid sewers of the subdivision, produced myriads of mosquitoes. These, after the first of June, were the attractions for the Nighthawks. They caught mosquitoes by flying close to the weeds and grasses.

After the Larks had closed their vesper recitative and the toads had begun to trill, the flickering white wing-bars of the Nighthawk were the only active bird elements in the evening dusk of the subdivision.

Chaetura pelagica. Chimney Swift. Through June and July the Swifts found good hunting in the air, high above the subdivisions.

Tyrannus tyrannus. Kingbird. Though there was no suitable nesting territory in the immediate vicinity, the King-birds frequently perched themselves upon a weed stem of the margins of the Lark territory. From one to three were noted frequently from June 5 to July 17, 1926.

Otocoris alpestris alpestris. Horned Lark. This northern relative of the Prairie Horned Lark may have occurred more frequently on the subdivisions than I have definite records for. During late February, in March and in April roving bands of Larks were noted long after the majority of *O. a. praticola* had established territories, and had mated. Most of these groups were too timid to allow approach sufficiently close for observation. They may have been *O. a. alpestris*, or *O. a. praticola* migrating to more northerly homes, or young *praticola* still unestablished and unmated.

However, on April 9, 1926, a flock of ten to fifteen seemed

decidedly larger than *praticola* and, though they would not allow close-approach (sentinels were posted while the majority fed) it is probable that these were *O. a. alpestris.* On April 24, 1926, the presence of this subspecies was definitely settled for a flock very similar to the earlier (twelve to fifteen individuals) allowed a group of us to approach within thirty to fifty feet. From that distance there was no question. The birds were appreciably larger and darker than *praticola* and their yellowish markings about the head (throat, forehead, superciliary line), so pronounced that it gave their head a brownish-yellow tinge even at one-hundred feet, whereas the impression of *praticola,* especially of males, is that of a generally whitish head, the yellow never being apparent until one is extraordinarily close and with good binoculars. Furthermore, the black markings of these birds seemed less pronounced than in *praticola,* probably through absence of contrasting white. When first we started toward them they remained for a moment quiet, but shortly were walking about and feeding on the heads of *Setaria* and *Amaranthus,* indifferent to our presence.

During our observation they passed near a brooding *praticola;* the male of the pair was on the sidewalk near, within twenty feet of the strangers. To them he paid not the slightest attention though an intruding *praticola* would have been ousted promptly and with vehemence. These Larks, of the same species so far as anatomy was concerned, were at that time and that place physiologically distinct. No kinship was recognized.

It is of great interest to speculate by what means ancestral history and environment had so modified these two forms, so closely related. Here was one, at home in northern Illinois, with a physiological cycle that prompted full song and pairing in February, nesting in March, renesting in April and with young now in the nest at the very time that these, so close northern relatives, were still roaming over his breeding home, in flocks, with no note but a mild "pseet," a month yet from their season of song, a thousand miles from their summer home.

Corvus brachyrhynchos brachyrhynchos. Crow. On April 16 the first crow was seen on the subdivisions, and records are frequent for the remainder of April, through May, June and July. Families were seen from June 20 on and these groups were frequently on the West Subdivision in July. What they

found as food on the Main Subdivision is not known but the ungathered corn of the West Subdivision was, undoubtedly, the attraction there.

Agelaius phoeniceus phoeniceus. Red-winged Blackbird. In the marshy land to the south of the subdivisions several Redwings nested but their occurrence on the area occupied by the Lark was adventitious or for food. The first was noted there March 31, 1926, and a few other records occur during the spring. The ungathered corn of the West Subdivision proved the chief attraction and accounted for most of the recorded visits.

Quiscalus quiscula aeneus. Bronzed Crackle. The subdivisions had but little attraction for the Grackle. This bird was seen on the area May 23, June 26, 28 and 30, and but one or two individuals in each case.

Loxia curvirostra minor. Crossbill. In the fall of 1925 the sunflowers along the drainage canal near the subdivisions were the source of food for small flock of Crossbills. Here they remained from November 8 to November 28, 1925, and were, a few times, noted in one or two of the small sunflower patches of the Main Subdivision.

Acanthis linaria linaria. Redpoll. In an area of evening primrose stalks and dead plants of white sweet clover two Redpolls were found December 22, 1925. They were the only birds upon the entire subdivision. In the same place four were seen on January 12, 1926.

Astragalinis tristis tristis. Goldfinch. Like the Crossbill, the Goldfinch fed also on the scattering sunflower patches of the Main Subdivision in the fall of 1925 and in mid-July, 1926, they went into ecstacies over ripe heads of goat's beard *(Tragopogon pratensis)* on the West Subdivision. They were noted on every visit from October 4 to November 28, 1925; appeared on the Main Subdivision for the first time on June 2, 1926, and frequently from that time to late July.

Spinus pinus pinus. Pine Siskin. On October 4 and 25, 1925, the Siskin was noted in large numbers on the sunflowers of the Main Subdivision.

Calcarius lapponicus lapponicus. Lapland Longspur. Here was a bird of the same mind as the Prairie Horned Lark, fully at home on the almost denuded, uninviting surface of the sub-

divisions in late winter and early spring. If the Longspur had bred here it, most probably, would have given the Lark a true ecological competitor in breeding territories.

The clear "dear" or "cheer" of the Longspur was heard for the first time on the Main Subdivision on January 12, 1926, on March 19 the bird appeared in large flocks; was noted again March 26, April 9, April 16, April 23 (the last a male in full breeding plumage). Again calls were heard April 28, and lastly, on April 30, throughout the entire morning as I sat in blind at a nest of the Prairie Horned Lark, large flocks wheeled back and forth above my head with their "chur-r-r-t, chur-r-r-t, chur-r-r-t, dear!"

Zonotrichia leucophrys leucophrys. White-crowned Sparrow. One only noted. It was taken in the ground trap, May 10, 1926.

Spizella monticola monticola. Tree-sparrow. The weed patches of the Main Subdivision attracted Tree Sparrows from October 25 to November 28, 1925, and from February 7 to April 30, 1926. On April 20, two were taken in the ground trap.

Melospiza melodia melodia. Song Sparrow. No Song Sparrows bred on the subdivisions but individuals occasionally ventured on from neighboring areas. Thus they were noted more or less frequently from May 21 to July 17.

Progne subis subis. Purple Martin. On April 23, 1926, the first appeared above the Main Subdivision. One again May 7, and from thence until late July they were feeding in the air above the area almost hourly.

Hirundo erythrogastrar. Barn Swallow. Like the Purple Martin, the Barn Swallow found good hunting over the subdivisions. From April 27 to July 5, 1926 their merry voices were rarely wanting. On July 3, a family of them found an old shed there and for three days they flashed in and out gossiping the while in their excitement over the discovery.

Riparia riparia. Bank Swallow. Noted over the Main Subdivision June 2, 4, 5 and 17, 1926.

Stelgidopteryx serripennis. Rough-winged Swallow. The only definite identification of this species was on May 6, 1926, though some of the records credited to the preceding May have been of this species.

Dendroica palmarum palmarum. Palm Warbler. Was noted in the weeds of the Main Subdivision October 4, 1925.

SUMMARY

This paper attempts to give the history of the Prairie Horned Lark as carefully and extensively as the literature, more than 220 visits to occupied territory, 33 nests, and over two years of study at Evanston, Ill., and Ithaca, N. Y. would allow. Visits were made to Prairie Horned Lark territory every month in the year. Thirty nests were followed daily from their discovery until they ceased to be occupied. The paper deals with a single bird subspecies yet so manifold are the fields against which such a subject impinges that even an extensive paper will miss some elements altogether, treat but briefly of many others, and cover thoroughly but a very few.

Summaries accompany most of the major sections of this treatise. Here will be considered only the more important points.

I. Range.

A. Extension of range. Henshaw erected the subspecies *Otocoris alpestris praticola* in 1884, splitting it from *O. a. alpestris.* Prior to this, records of a new form of Lark and new Lark breeding records were published from lower Ontario and New York. These were variously interpreted as a "paler form" or as southward extensions of *O. a. alpestris.* Following 1884 a consistent and progressive series of records demonstrated that the Prairie Horned Lark, coming up probably from Michigan through Ontario, invaded successively New York, Vermont, Massachusetts, New Hampshire, Maine and Connecticut. From New York or Vermont it seems to have invaded Quebec much later; and lastly on the north, (probably from New England states) New Brunswick, Prince Edward Island, and Nova Scotia. Shortly after its entry into New York, the Lark appeared in western Pennsylvania, then farther east in that state, and south into Maryland and West Virginia. Less complete evidence seems to show that Indiana, Michigan, Ohio, probably northern Kentucky, and southern Missouri have been occupied by this Lark since white man has entered and altered those regions. The regular advance of the bird, always consistent with geographic conditions, is suggested as an irrefutable evidence that

such an extension is *bona fide.* It is suggested that this extension of range has resulted from changes which civilized man has made by deforestration and cultivation; thus creating permanent, or seasonally semi-barren, conditions which the Prairie Horned Lark required.

B. Primitive range. It is noted that the dryer portions of the prairies of Illinois have probably long been occupied by this Lark. The studies of Forbes and Gross seem to indicate that the Lark, though it probably breeds in Lower Austral, Upper Austral and Transition Zones, seems to prefer the Transition in that state. It is suggested that the prairies of northern Missouri, Iowa, Wisconsin, Minnesota, eastern portions of Kansas, Nebraska, North and South Dakota and southern Manitoba, probably formed the ancestral home of the subspecies. Nearly all of this vast region would have been suitable for two broods in March, April and early May, though the bird would have been forced to the more barren regions as the grasses became vigorous in late May, June and July. That this Lark species is versatile in the matter of occupation of new territory seems to be further demonstrated by the observations of Gatke and Saunders in Europe with regard to *O. a. flava.*

II. Migration.

A. General. Subspecies of the Horned Lark vary from strictly sedentary forms to others which leave their breeding range entirely and for long periods, and therefore are quite highly migratory. The Prairie Horned Lark, in migratory habits, lies between these extremes. This bird breeds north to the southern edge of Canada, migrates south to South Carolina, Kentucky and Texas. From the northern part of this range it is absent during the month of December and part or all of January. Throughout the remainder of the breeding range some individuals will be always present.

B. Migration of sexes and individuals. Insufficient data on this subject seem to indicate that resident adult males arrive first on the breeding ground, next resident adult females, next transient males and females and lastly vagrants and immature.

III. The Lark in Autumn and in Winter.

A. Flocking. Young Larks flock shortly after nest leaving. If the breeding ground has become untenable due to vegetation

they seek other regions. Flocks grow larger through additions of adults in August and September and then smaller as migration begins. In flight the flocks are comparatively compact but they spread widely when the birds alight to feed or pass the night.

B. Habitats. Larks in autumn and winter occupy regions essentially like those in which they breed in March and April, viz., semi-barren or almost denuded conditions which may be natural or due to some seasonal condition of agriculture.

C. Associates in fall and winter. The Lapland Longspurs and the Shore Larks *(Otocoris alpestris alpestris)* are the only other birds which occupy conditions like those in which the Prairie Horned Lark occurs in fall and winter.

D. Food in fall, winter and early spring. Observations of the writer indicate that food during these seasons is very largely weed seed and waste grain. These are in essential accord with the more extensive investigations of McAtee (1905).

E. Call notes. Usually "p-seet" when on the ground; in flight usually "p-seet-it"; when flushed "zu-weet", "sur-reet", "zeet-eet-it" or "zeet-it-a-weet".

F. Flights. Short flights: choppy undulation of three or four rapid, even strokes, interrupted by space of two wing beats when wings are closed; note uttered on the climb of the undulation. Prolonged flights: one, two or three long strokes are made with pause of about one wing beat between each stroke with wings folded; then four to six rapid and successive strokes which cause a climb; note uttered on the climb.

IV. Reproduction.

A. Breeding Habitats.

1. General. The literature shows a surprisingly large range of habitats in which the Prairie Horned Lark has been known to nest. These habitats, resulting in the range of this Lark for the most part from agricultural activity or other human agencies, are those which most nearly result in barren conditions. It does not matter that these barrens may be seasonal or otherwise very temporary, if they are suitable for the initiation of nesting. That bare ground is the determinant is shown by the fact that variations of moisture, soil, elevations and temperature will all

be tolerated, in the selection of nest sites. The Prairie Horned Lark does not differ greatly in the ecological condition of breeding habitats from other Horned Lark subspecies.

2. The breeding territory at Evanston, Illinois. Some typical Chicago marsh, in the Evanston region, was drained for a golf course. The golf course was later cut up into real estate subdivisions; sewers were laid exposing a wide area of bare soil in the streetways; old sand hazards remained here and there. This series of activities provided nesting sites for many Larks. More than a score of nests were located on this area (about 90 acres) in 1926.

A plot of vegetable gardens, bordering the region noted above on the west (where Larks probably had nested for some years), was also subdivided and the vegetation subsequently neglected. Here several Larks also nested.

The advent of vegetation in both areas and the demand of the Lark for bare ground, forced a seasonal succession of Horned Lark breeding sites first from lot surface, to streetway, to sand hazard, to vegetable garden, in the order that each was successively occupied by verdure.

3. The breeding territory at Ithaca, New York. One nest was located on the overturned sod of a former hay meadow. Most of the observations were made on a tract of ground that was largely fall wheat, partly fall rye, and the remainder devoted to experimental vegetable gardens. The growth of the fall wheat forced the Larks from its surface by late May. The gardens, and portions of the fall rye area which were turned under as green manure, remained suitable throughout. Clean vegetable gardens will always present a considerable amount of bare soil and the Prairie Horned Lark is usually able to occupy them until late June.

B. Song.

1. Season of song. Extended, in the Evanston region, from mid-January until early July; in the Ithaca region, from mid-February to late June.

2. Monthly variations in song numbers. Using flight songs for a criterion, it was found that May was the optimum month. The Lark sings, both from the ground and in the air, under all conditions of weather, though flight songs are most numerous on

quiet, mild days; perhaps a little more numerous when the sky is overcast than when it is clear.

3. Variations in song through a nesting period. Most vigorous period of song extended through nest building, egg laying and incubation. Perhaps of this period that portion of it when the female incubated allowed most song from the male since he attends the female carefully during nest building and egg laying. Period of least song occurs when young are in the nest, for the male assists in feeding.

4. Variations in song throughout a day. Ground songs are regularly distributed throughout the entire day; flight songs seem to be most numerous toward noon and near sundown.

5. The relation of the song of the Lark to that of other birds. For three months the Prairie Horned Lark is the only singing bird in the open field; with the coming and establishment of other migrants in late May and June many other songs will be heard in that region. On June 16, 1926, the Horned Lark, the last to begin song, went into flight song at 4:00 A. M. The Lark, however, almost always closed the singing at night with a long period of recitative which in mid-June, would not close until after 8:00 P. M.

6. Description of song. The literature contains several descriptions of the flight song of the Prairie Horned Lark, that of Langille (1892) seeming to be most accurate. He describes the flight. The song he describes as "quit, quit, quit, you silly rig and get away". This is the intermittent type; nowhere in the literature has a description of the recitative been found.

7. Types of song. Songs are sung from the ground, from a clod or any other slight elevation, the greatest elevation being the roof of a sample apartment put up on the Evanston area; and from the air. The ground songs are similar to the flight songs though rarely as long or as systematically presented.

The urge to flight song may come at any time or after an invading male Lark has been evicted from occupied territory. Larks will also go into flight song upon the approach of a human or they can be forced to go up by driving them for a time about their territory.

The climb to flight song is distinctive and usually executed without a sound from the bird. The songs, in the air, are of two types: a recitative or rapid monotony of notes usually

uttered at the beginning of the flight song, though occasionally at other periods, never over a few seconds in duration, accompanied by a steady beat of the wings; an intermittent uttered while the Lark sails, about two seconds in duration, followed by a somewhat longer silent period during which the Lark flutters up. The recitative can be transcribed as "pit-wit, wee-pit, pit-wee, wee-pit"; the intermittent as "pit-wit, pit-wit, pittle wittle, little, little, leeeeee". Large rough circles are described overhead during the flight song or the bird heads into the wind if it is strong. The Lark closes flight song by a headlong drop to earth with wings tightly folded.

Female Larks seem to be unaware of the males in flight song though other males note the bird overhead. The territory which a bird may occupy in flight song is very extensive. Never were two visible birds noted in such a performance simultaneously. The one in the air is left undisturbed though his performance may carry him over many other Larks breeding grounds below. Breeding territories are not vertical for a distance above a few feet; the flight song territory is something quite different.

8. Quantitative studies of song.

a. Height of the Lark in flight song. Of several methods employed to determine the heights of Larks in flight song the most accurate was found to be the use of a binocular with an ocular scale. It was determined thus, through measurement of 25 songs, that the Lark sings from elevations that vary from 270 to 810 feet. The average was 464.4 feet. Differences in height seemed to be individual variations or due to weather.

b. Duration of the flight song. Thirty timed flight songs varied from one minute to five; the average was 2.34 minutes.

c. Number of songs per minute during the flight. Intermittents, regularly given, averaged 11.9 per minute.

d. Relation of the singing male to the incubating female. An Evanston, Illinois, bird sang from song posts on the ground which, during one entire day, varied a few feet from the incubating female out to 100 yards. The average was 38.66 yards. Ithaca birds, with bigger territories, sang frequently as far as 150 yards from the nest.

C. Nesting territories.

1. At Evanston, Illinois. A breeding territory was delimited by a male Lark on February 7, 1926, at Evanston, Illinois. From his selected territory he could not be driven. This territory was about 100 yards square. Late March snows disrupted all territories and it was not learned here whether the original sites were ultimately resumed or whether the same territory was maintained through more than one nesting. The pressure of vegetation in late May and June greatly modified the territories at Evanston and caused, eventually, the abandonment of most of those on the erstwhile golf course.

2. At Ithaca, New York. A male Lark was forced to mark territory for the first time on March 13, 1927, though it had undoubtedly been established some time before this. Territories voluntarily marked were somewhat larger than those indicated when the birds were forcibly driven out. The regions of a breeding territory most frequently occupied were those boundaries which joined the territories of a neighboring Lark.

The territories at Ithaca were much larger than those at Evanston. (Possibly due to fewer Larks attempting to occupy them.) At Evanston they were seldom over 100 yards square, at Ithaca they ran out to lengths of 300 yards, and widths of 200 yards, in March and April.

In general all suitable territory was occupied at Ithaca and most boundaries were established by the margins of unsuitable areas (see Figures 2, 3 and 4), though a large amount of suitable territory, extending north of territory "C", was used only in part by this bird.

Boundaries between males were often definitely established on ground that had no natural marker whatsoever.

3. History of territories in subsequent nestings. The territory history of three pairs of Larks was followed from March to June at Ithaca. One influence only modified the territories, viz., the growth of vegetation. Territory "A", entirely on fall wheat, was abandoned completely by the close of the second nesting in May. Territory "B", in part on fall wheat and in part on the gardens, was gradually reduced to the gardens, from an area once 300 by 200 yards to an ultimate area about 100 by 50 yards. Territory "C", almost entirely on the gardens, suffered no major

reduction. But "C", whose territory abutted that of "B", gave no ground to the latter.

4. Feeding in relation to nesting territories. Though most of the feeding was done on the nesting territories, a neutral feeding territory was discovered and others were indicated because, now and then, the Larks would go off on purposeful flights entirely out of their areas.

5. The relation of the female to the nesting territory. The female would mark the same territory as that marked by the male and she, if anything, was more closely restricted to it than the male. She selected the nest site with little or no regard to the center of the area.

D. Courtship.

1. Fighting. Prior to the establishment of well-defined territories, fighting between males is promiscuous; after that, fighting takes place only on territory boundaries, where two Lark areas juxtapose. The males, at the boundary line, frequently strut before each other and often peck the ground furiously, like barnyard cocks, but all fighting is in the air. On a boundary this fighting often results in a curious game of tit for tat as the male Larks chase each other back and forth. Every adventitious Lark, wandering into established territories, is promptly evicted by the male. Such a bird will leave without protest. So far as noted the female is never the direct cause of fighting, in fact fighting is most frequently noted when the female is brooding and the males are no longer attending her. Only once was a female noted to drive out another Lark, a male. She was defending a recent nestling.

2. Reactions of male and female to each other. The female has no courting maneuvers and was never observed to sing. Only once was she seen to importune sexual attention and then by a crouch and flutter similar to the actions of the female House Sparrow. The male struts frequently before the female with wings dropped, tail spread and horns up. He will assume this attitude before another male at the territory boundary.

Attention is drawn to the discrepancy between these observations of territory, possession of territory, fighting and significance of fighting, and those of many previous and some recent writers who have been inclined to give to the actions of these birds an unwarranted anthropomorphic significance.

E. The nesting.

1. Season of nesting. The literature contains four February records of nests and many records of March nests in many states, and two or three records of nests in July. The writer has records of nests from about March 21 to July 12, in 1926, at Evanston, Illinois; from about March 11 to June 28, 1927, at Ithaca, New York.

2. Explanation of March nests. It is suggested that such a strange phenomenon as that of a Passerine bird nesting in March cannot be explained easily. The bird has too long a nesting season to explain it on the conditions that might exist in early spring alone; and then, in the range where the Prairie Horned Lark was studied, nests are frequently destroyed by inclement weather and many young die of starvation at this season. Since this bird demands barren conditions, and not verdure, for a nest site, the conditions are suitable very early and it is suggested the early-nesting physiological cycle may have been acquired in a more propitious climate and subsequently carried north and east. It is further noted that *O. a. actia* of California nests in March where conditions are quite ideal.

3. Weather control of March and April nests. With one exception, all observed nests (a total of fourteen) of March and April were not begun until the mean temperature rose above 40 degrees Fahrenheit for two or more days in succession. The exception was the initiation of a nest on the *first* day that the temperature rose above a mean of 40 degrees Fahrenheit. Once weather conditions, suitable for the initiation of nesting activities, prevailed, no subsequent weather, no matter how severe, (excepting deep snow only) would inhibit these activities. Even birds that had nested in March and whose nests were destroyed by late March and early April snows, would not renest until weather conditions were as given, though this necessitated a delay of nearly three weeks in two cases at Ithaca, N. Y. That this was a delay caused by the weather is easily demonstrated by the fact that an exceptional case (noted above) began renesting on a single suitable day, but two other Larks waited two weeks longer for renesting when weather again was suitable and for a longer period. (See Figure 8.) It is known that two of these birds, and probably all, had had former nests.

On the basis of this known weather control it was possible to

calculate the frequency, over a period of years, with which nestings would occur in March, by a study of weather summaries for the month. The results showed one year when nesting was impossible and sixteen years of possible nestings, at Evanston, Ill. (For the years 1910 to 1927, inclusive, excepting 1924.) During ten of the sixteen years nestings could have been successful; during two they would have been destroyed by snow; and during four, weather and snow would have made success problematical. At Ithaca (for the years 1916 to 1927 inclusive) the summaries showed one year when nests were impossible and eleven years of possible March nests. During five of the eleven years, nesting could have been successful; during four they would have been destroyed by snow; and during two their success would have been problematical. Summaries could not be obtained for years previous to the earliest here noted. On the basis of those obtained it is shown that northern Illinois has more favorable weather in March than Southern New York. New York, it is to be remembered, is a state recently occupied by the Lark.

It is concluded that three or more inches of snow, lasting two or more days, would destroy a nest.

4. On finding nests and the reaction of nest-building and egg-laying Lark. It is suggested that the discovery of nests during nest building is possible by locating first the calling or singing male. At this period the male will be attending the female closely and she will be discovered shortly. The status of nesting can always be determined by the actions of the female. During nest building she is very restless, runs here and there, flies up and away, but shortly returns. Eventually she may disclose the site of the nest excavation. These reactions are instinctive responses to the desire for nest concealment. All nest building seems to be done by the female.

During egg laying the discovery of a nest is at best accidental. Neither male nor female has been noted to approach a nest during this period. They express no solicitude beyond that of nest concealment, which is a remarkable nonchalance, especially on the part of the female. This reaction is so marked that an observer can nearly always be assured of the status of nesting whenever it is noted.

When incubation has begun the behavior is very different, as is also the behavior after the eggs have hatched. These reactions

will be noted below. During these periods nests may be located by a systematic search that involves first, driving the male about until the female is noted (she will flush from the nest and the male will go to her), then a patient watch of the female will, after a variable length of time, disclose the nest. When young are being fed the male will, at times, disclose the nest much more quickly than the female, for he assists in feeding and has nest-concealing instincts that are very poorly developed. Though the nest of the Prairie Horned Lark is never concealed from above, it fits its semi-barren environment so closely that a promiscuous search over a breeding territory is nearly always tiresome and unavailing. An incubating or brooding Lark, as will be discussed below, often remains close to her nest when the day is chilly or in the very early morning or toward evening. Nests can be found under these circumstances by a systematic search of likely habitats and so flushing the bird from the nest.

5. Nest building. No evidence of the use of a natural depression was noted either at Evanston or at Ithaca, all were dug by the female. According to Sutton (1927) and observations which the writer has made of *O. a. strigata* in western Oregon, this excavation is dug with both beak and feet. The nest is constructed, usually, at the edge or partially under a grass tuft or clod which, in the case of the Prairie Horned Lark, lies most frequently on the west, northwest or north (see Tables 3, 4, 7 and 8) possibly because the cold and violent winds, of the early nesting season, come from this region. The body of the nest consists of coarser stems and leaves with a finer lining within. The time spent in nest construction varies from two to four days.

6. Seasonal variations in nest structure. The evidence shows that any seasonal variation in nest structure is due to variations in available material and has nothing to do with variations in "necessity" or "onerous duties".

7. "Paving". The majority of the nests of the Prairie Horned Lark showed a variable amount of clods, pebbles or similar items, laid about the margin usually on the side away from the protective tuft or clod. These so-called "pavings", were, again, always composed of the material most easily obtained regardless of the permanency of such. It is suggested that the purpose of "pavings", if there is a purpose, arises from the method of nest

construction and from the desire of the Larks to have a bare ground nest-approach.

8. Eggs and egg-laying. The egg is described as having a background of grey with an occasional greenish tinge, which background is almost completely concealed with a fine speckling of cinnamon-brown. The cinnamon-brown often forms a denser ring about the larger end. Several other variations are noted. The average size was found to be 2.25 cm. by 1.55 cm. The eggs of natural second sets seemed to be a trifle larger than first sets of the same individual. The number of eggs per set varied from two to five; the average is about four; the smaller sets occurred early, the larger sets later.

9. Incubation period. The optimum was determined to be eleven days. Only the female incubates.

10. Reactions of female and male Larks during incubation period. The male shows little or no nest solicitude during the incubation period. The female has a highly developed series of automatic instincts of solicitude which are modified by time of day, condition of weather and frequency of disturbance. The most highly developed and probably the most recently acquired of these has been given the name "nest concealment by abandonment", or "casual abandonment". The female leaves the nest, in this reaction, when an intruder is at a long distance, and flies quietly away, low against the ground, and does not show other solicitude for a very considerable period. The distances of the intruder from the nest during this reaction vary from 25 to 100 yards or often farther, a greater distance, it will be noted, than would disturb even a timid Lark under other circumstances. A reaction, that in many ways is the reverse of this, but still a marked exhibit of solicitude, is that called "distress simulation". The "distress simulation" consists of a precipitate flushing and rapid flutter over the ground after the nest has been approached closely. This reaction would be given most frequently on very cold days, in the dusk of very early morning or evening and when the bird was flushed very shortly after a return to the nest. This reaction is certainly more primitive than the first here described and is probably a culmination of the more frequent distraction display that most birds present when their nests are disturbed. Between "concealment by abandonment" and "distress simulation" a complete gradation occurred which, since the

reactions are exact opposites in expression, involved a curve which dropped from the first to the zero point and then rapidly ascended to the expression of the latter. Thus between the two, lessened expressions of either reaction would result, with a curious hiatus midway in which the incubating bird would allow an intruder to approach closely and then leave without an expression of either. Experimental flushing of an incubating bird from a blind showed that the bird, in one case, would give distress simulation if flushed in an interval that was less than two minutes from the time of her return; but would give casual abandonment if flushed after an interval of five minutes. (See Table 14.) A female Lark, shortly after being forced from a nest, would express her agitation by aimless ground pecking, and, to be sure, would eventually be driven by the incubation urge to return to the nest even though an intruder might be much nearer than the distance when the nest was originally abandoned. This complex of instincts involved both the urge to incubate, and the urge to protect. The instincts to protect, by whatever method, would all be overshadowed in time by the instinct to incubate.

F. The young.

1. Hatching. With the exception of those nests of early April, in which incubation began before the set was complete, all young hatched within an hour or two of each other. The young are fed within an hour or two following hatching.

2. Feedings. In most cases the male assisted the female in feeding the young. In carefully observed cases he visited the nest less often, but brought greater burdens and fed more young at a visit than did the female. The total number of feedings during one day (April 30, 1926) was 117. An extensive summary is presented in Table 17.

3. Food of nestlings. Observations of the adults and dissection of a few nestlings showed that some vegetable matter (weed seeds) is fed in early spring, but that even in March most of the food is animal matter. Later in the season grasshoppers become conspicuous in the diet. The adults dig up both cutworms and earthworms.

4. Reaction of adult Larks with young in the nest. The male shows solicitude for the nest and its contents for the first time after the hatching of the eggs. His solicitude is restricted

to calls. The female will leave her brooding in typical "concealment by abandonment" when conditions are appropriate as when incubating; likewise she will go from the young in "distress simulation" under circumstances as noted above. Proportionately the number of "concealments by abandonment" decreases and "distress simulations" increase slightly. Other reactions, which are various primitive expressions of solicitude, or intermediates of the above two, increase proportionately (see Tables 11 and 13). Perhaps the return of more primitive instincts indicates a sum total of greater solicitude. Since the female is frequently absent from the nest in food foraging, she will come in, as an intruder approaches, with calls and cries.

One or two references in the literature show that the reactions to dogs is the same as to man, but hens were driven off by entirely different methods.

5. Nest cleaning. The Larks removed all excreta throughout the full extent of nest occupancy. Much of the excreta was eaten by the adults early in the season and dropped to the ground fifty or more feet distant later. It is suggested that this seasonal change of habit may have been related to the available food supply. The instinct compelling excreta removal proved itself very strong, at times overcoming strong solicitude for nestlings, and even fear.

6. Developmental reactions of the young. The young showed a psychic development closely related to their rate of growth and not to their age. Young which were of the same age or but one day younger than their nest-mates often presented a psychic development two to four days behind them. This was due to uneven feeding which occurred frequently in the early spring, because of uneven hatching or an inadequate food supply.

Normal nestings give a food response indiscriminately up to the fifth or sixth day. Just prior to this time their eyes open. Following this they respond not at all or momentarily only. They withdraw at a touch from the hand on the sixth day and sink back quietly into the nest in "crouch-concealment" between the seventh and ninth days. Upon being removed from the nest at this age they sit quietly upon any object upon which

they are placed; prior to this time, they wriggle about when taken from the nest. They leave the nest on the tenth day and now they express fear by hopping and calling wildly when disturbed. An expression of this type of fear, prior to the tenth day, would take them from the nest prematurely.

7. Growth of the young. Tables 18, 19, 20 and 21, together with Figures 12, 13, 14, 15, 16 and 17, give extensive statistics of growth of weight, length, length of tail and length of flight feathers. A lessening in weight growth occurs, normally, between the seventh and eighth days. This is brought about by the simultaneous unsheathing and drying of most of the feathers. On the other hand growth in length shows, if anything, an acceleration at this period due to the extension of the tail. Marked variations in growth occurred in the various broods measured and in the different young of the same brood. This was brought about by two things: the fact that a slight difference in age gave the older Larks a great advantage in securing food from the parents; and the fact that food was more plentiful later in the season than at the beginning.

Weight growth curves show a gradual increase over the first three days, a very precipitate rise (except for April nestlings), for the next three or four days, a marked levelling during seventh and eighth (in one case the sixth), and a gradual rise during the ninth and tenth. Nestlings in May grew slightly more in the same period than a nestling in June and much more than a nestling in April. This decrepancy of growth seems closely (though perhaps indirectly) correlated with the temperatures of these seasons.

Length growth curves show a precipitate rise during the first three days, a slight levelling during the next three days, and a precipitate rise during the sixth, seventh, eighth, ninth, and tenth days. The cause for the intermediate levelling is not understood, but the rise toward the end of the nesting period is brought about by the growth of the tail.

8. Descriptions of the young at various ages. The recently hatched nestlings are rather heavily covered with down (a necessary protection against sun and cold in their exposed location). The down is cream-buff in color. At nest-leaving age the young Lark is completely feathered, but presents an appearance quite unlike that of the adults; each feather of

the upper surface has a triangle of brown at its tip, the under surface is white except the throat, which is grey.

9. Enemies. In the early breeding season the enemies of the young are weather and a scanty food supply. The weather may result in snows which bury them from sight. The scanty food supply may result in the starvation of one or more of the nestlings. Starvation results from the automatic feeding reaction of the adults wherein the nestling nearest that part of the nest which is habitually approached by the adults will receive the first feeding; if the food is scanty this bird will receive nearly or all of the food. Only when food is so abundant that the first nestlings fed do not swallow promptly will the remainder of the brood be fed. In this case food is withdrawn from the first mouths and put in the next and so on (as Herrick, in "Home Life of Birds" has shown). The female Lark rarely brings more than will go into one mouth; the male may feed two or more, but never four or five at a time. Those young Larks that have a few hours advantage in hatching (a full day in several cases in the early spring), will have the advantage in size that will allow them to push to that side of the nest over which the food always comes. They survive, the others may perish. Such occurred in many observed nestings in April.

Predacious enemies cause a greater and greater loss as the season advances into June and July. The optimum season is shown to be May.

10. The Cowbird and the Lark. One case of Cowbird parasitism was observed and followed. A Lark, which hatched before the Cowbird, came to maturity. The Cowbird probably did not. It is suggested that the early nesting season and the exposed habitat may mitigate against such parasitism as may also the early departure of the young Larks from the nest. However, the adult Lark will tolerate the parasitism, the food of June and July is suitable, so that other reasons prevent more extensive parasitism at this later season.

11. Protection of the young. The young leave the nest, normally, on the tenth day, some three to four days before they can fly. Their protection during this interval is silence and a very effective "freeze" or "crouch-concealment." Their plumage is remarkably adapted for this. The actions of the

parents, especially the female, with her "abandonment concealment" are calculated to take advantage of the protective color of nest and young at all ages.

12. Nest leaving. Young leave the nest usually by following a parent that has brought food. One case was noted wherein the female enticed a belated nestling from the nest with a food morsel. The young fly in about five days after leaving the nest. They hop for some days after nest leaving whereas the adults walk. This hopping may be anatomical or an atavism.

V. Molt.

Dwight (1890) showed that juveniles and adults have a complete molt in late summer. Breeding plumage is acquired by the wearing off in late winter of the brown tips that obscure the areas of black.

VI. Ecology of the Nesting Site of the Prairie Horned Lark in Relation to Other Breeding Birds at Evanston, Ill.

Throughout March, April and most of May the Prairie Horned Lark is the only breeding bird in the open field. The growth of verdure at Evanston, Ill., presented such a range of conditions that nine species and about 74 pairs of birds were occupying it in June, however. Though most of the Larks had been driven from it by this change of conditions, a few remained in the barer areas. A category of these breeding birds, listing their nest sites in descending order from the heaviest vegetation to the scantiest, gave the following: Dicksissel, Bobolink, Savannah Sparrow, Meadowlark, Vesper Sparrow, Prairie Horned Lark. The Vesper Sparrow, as well as the Prairie Horned Lark, suffered a seasonal modification of nest site and was obliged to move for later broods, about two weeks of plant growth behind the Lark. Comparisons of many other habits are also noted.

VII. Non-breeding Birds That Fed on or Above the Territory Occupied by the Prairie Horned Lark at Evanston, Ill.

Twenty-eight non-breeding species of birds were noted feeding on or above the Evanston territory. Of these the most interesting were the Lapland Longspurs that occupied it with Larks in

late winter and early spring; and the Shore Lark *(O. a. alpestris)* that was noted in April. To the Shore Lark the breeding Prairie Horned Lark was indifferent, indicating that this latter bird did not recognize the former as being of the same species.

CONCLUSION.

To one, who watched the Prairie Horned Lark on its home in the biting winds of January to the sultry sun of mid-July, no word fully expresses the deep impression made. To one, who has followed the vicissitudes of its life history through ever-changing seasons, interest in the bird becomes the more intriguing. Just a subspecies of a single species it is, but to one who would look deeply into its inner secrets, not even words in thousands express adequately the findings.

BIBLIOGRAPHY.

Allen, A. A. "The Red-Winged Blackbird; A Study in the Ecology of a Cat-Tail Marsh," Proc. Linn. Soc. N. Y., 1911-13, 77-86.

——"Daisy Fields in June," Bird Lore 25, 1923, 211.

——"Observing Birds at Close Range," Bird Lore 27, 1925, 206.

Allen, J. A. "Early Nesting of the Shore Lark Near Indianapolis, Ind.," Bul. Nut. Ornith. Club. 3, 1878, 189.

Allen, J. A., and W. Brewster. "A List of Birds Observed in the Vicinity of Colorado Springs, Colorado, During March, April and May, 1882," Bul. Nut. Ornith. Club 8, 1883, 193-195.

Attwater, H. P. "List of Birds Observed in the Vicinity of San Antonio, Bexar County, Texas," Auk 9, 1892, 237.

Bailey, F. M. "Handbook of Birds of Western U. S.," Boston, Houghton Mifflin Co., 1908, 267.

Bailey, W. L. "Summer Birds of Northern Elk County, Pa.," Auk 13, 1896, 294.

Baird, S. F., T. M. Brewer and R. Ridgway. "A History of North American Birds," 2, 1874, 142.

——"North American Birds," 2, 1875, 144-145.

Barnes, R. M. "List of Birds Breeding in Marshall County, Ill.," Ornithologist and Oologist, 15, 1910.

Barrows, W. B. "Michigan Bird Life," Bul. Dept. of Zoo. and Phys. Mich. Ag. College, 1912, 408-409.

Batchelder, C. F. "Winter Notes from New Mexico," Auk 2, 1885, 239.

Bergtold, W. H. "A Study of the Incubation Periods of Birds," Denver, 1917, 97.

Bigelow, H. B. "Birds of Northeastern Coast of Labrador," Auk 19, 1902, 29.

Blincoe, B. J. "Birds of Bardstown, Nelson Co., Kentucky," Auk 42, 1925, 411.

Brewster, W. "The Prairie Horned Lark *(Otocoris alpestris praticola)* on the Coast of Mass.," Auk 5, 1888, 111.

——"Second Occurrence of the Prairie Horned Lark in Eastern Mass.," Auk 6, 1889, 71-72.

——"Breeding of the Prairie Horned Lark *(Otocoris alpestris praticola)* near Pittsfield, Mass.," Auk 11, 1894, 326-327.

Brimley, C. S. "Some Additions to the Avifauna of North Carolina With Notes on Some Other Species," Auk 10, 1893, 243.

Brooks, E. A. "Notes from West Virginia," Auk 25, 1908, 235-236.

Brown, W. J. "Prairie Horned Larks," The Ottawa Nat. 20, 1906, 41.

Bruner, L., R. H. Wolcott and M. H. Swenk. "A Preliminary Review of the Birds of Nebraska," 1904.

Burleigh, T. D. "Notes on Bird Life in Allegheny County, Pa.," Wil. Bul. 35, 1923, 90.

Butler, A. W. "The Birds of Indiana," 1897, 875.

Cameron, E. S. "The Birds of Custer and Dawson Counties, Montana," Auk 24, 1907, 392.

Carroll, J. J. "Notes on the Birds of Refugio County, Texas," Auk 17, 1900, 345.

Chapman, F. M. "Notes on the Plumage of North American Birds," 50, Bird Lore 20, 1918, 349, 350.

——"Handbook of Birds of Eastern North America," D. Appleton and Co., 1923, 349.

Cook, A. J. "Birds of Mich.," Mich. Ag. Exp. Sta. Bul. 94, 1893, 84.

Cooke, W. W. "The Horned Lark in Georgia," Auk 25, 1908, 318.

——"Some Winter Birds of Oklahoma," Auk 31, 1914, 182.

Coues, E. "Birds of the Northwest," Dept. of Int. Misc. Pub. 3, 1874, 37-40.

Criddle, N. "Notes on the Nesting Habits and Food of the Prairie Horned Lark in Manitoba," Canadian Field Nat. 34, 1920, 14-16.

——"A Calendar of Bird Migration," Auk 39, 1922, 42.

Criddle, S. and N. "Horned Larks at Aweme, Manitoba," Ottawa Nat. 30, 1917, 144-148.

Crone, J. V. "The Prairie Horned Lark," Oologist, 6, 1889, 231.

Dadisman, A. J. "Prairie Horned Lark," Bird Lore 21, 1919, 181.

Davie, O. "Nests and Eggs of North American Birds," Columbus, 1889, 254-255.

Davis, Fred J. "Nesting of the Horned Lark *(Eremophila cornuta)* in Central New York," Oologist 4, 1878, 9.

Davison, J. L. "The first nest and eggs of "*Eremophila alpestris* Found in Niagara County, New York," Auk 2, 1885, 217-218.

Demille, J. B. "Birds of Gaspe County, Quebec," Auk 43, 1926, 519-520.

Dibble, E. B. "The Feeding of Young Horned Larks," Bird Lore 2, 1900, 117.

Dionne, C. E. "Catalogue des Oiseaux de la Province de Quebec, etc.," 1906, 270.

Dugmore, A. R. "Bird Homes," New York, 1902, 40-41.

Dutcher, W. "Bird Notes from Long Island, N. Y.," Auk 5, 1888, 180.

Dwight, J., Jr. "The Horned Larks of N. A.," Auk 7, 1890, 138-139.

——"The Prairie Horned Lark in Northern Pa.," Auk 9, 1892, 202.

Eaton, E. H. "Birds of New York," N. Y. State Mus. Mem. 12, 1914, 203-206.

Eifrig, C. W. G. "Birds of Allegany and Garrett Counties, Western Maryland," Auk 21, 1904, 238.

——"The Birds of Ottawa," Ottawa Nat. 24, 1911, 187.

——"In the Haunts of Cairn's Warbler," Auk 37, 1920, 555.

——"Prairie Horned Lark *(Otocoris alpestris praticola)* in Maryland in Summer," Auk 40, 1923, 126.

Eifrig, G. "Northern Birds of Cumberland, Maryland," Auk 19, 1902, 212.

Everman, B. W. "Birds of Carroll Co., Ind.," Auk 6, 1889, 23.

Faxon, W. "The Prairie Horned Lark *(Otocoris alpestris praticola)* Breeding in New Hampshire and Massachusetts," Auk 9, 1892, 201.

Faxon, J. "Early Nestings of the Prairie Horned Lark," The Ottawa Nat. 14, 1900, 23.

Fleming, F. H. "A List of the Birds of the Districts of Parry Sound and Muskoka, Ontario," Auk 18, 1901.

——"Birds of Toronto, Canada," Auk 24, 1907, 77.

Forbes, S. A. "The Mid-Summer Bird Life of Illinois: A Statistical Study," Am. Nat. 42, 1908, 505-519.

Forbes, S. A. and Gross, A. O. "Numbers and Local Distribution in Summer of Illinois Land Birds of the Open Country," Bul. Ill. Nat. Hist. Survey Div. Dep. of Registration and Ed. 14, 1922, 187-218.

Forbush, E. H. "The Horned Lark," Bird Lore 13, 1911, 322-325.

——"Birds of Mass. and of Other New England States," 2, 1927, 365-373.

Gätke, H. "Heligoland as an Ornithological Observatory," Edinburgh, 1895, 363-368.

Goss, N. S. "History of the Birds of Kansas," Topeka, Kan., 1891, 374.

Gross, A. O. "The Dicksissel *(Spiza americana)* of the Illinois Prairies," Auk 38, 1921, 10.

Hatch, P. L. "Notes on Birds of Minnesota," Biol. Ser. 1, 1892, 259.

Harlow, R. C. "Notes on the Breeding Birds of Pa. and New Jersey," Auk 35, 1918, 136.

Harris, H. "The Season: Kansas City Region," Bird Lore 24, 1922, 159.

Hegner, R. W. "The Prairie Horned Lark," Bird Lore 1, 1899, 152-154.

——"Where Does the Male Horned Lark Stay at Night?" Bird Lore 11, 1909, 75-76.

Henshaw, H. W. "The Shore Larks of the United States and Adjacent Territory," Auk 1, 1884, 255-268.

Hess, I. E. "One Hundred Breeding Birds of an Illinois Ten-mile Radius," Auk 27, 1910, 25-26.

Howard, H. E. "Territory in Bird Life," New York, 1920.

Howe, R. H. and G. N. Allen. "Birds of Mass.," 1901, 81.

Howell, A. H. "A Prelim. List of the Summer Birds of Mount Mansfield, Vermont," Auk 18, 1901, 341.

——"Notes on the Summer Birds of Kentucky and Tennessee," Auk 27, 1910, 297.

Howey, J. M. "Breeding of the Shore Lark in Western New York," Bul. Nutt. Ornith. Club 3, 1878, 40.

Isley, G. "A List of the Birds of Sedgwick Co., Kansas," Auk 29, 1912, 36.

Jones, L. "The Prairie Horned Lark," Wil. Quart. 4, 1892, 54-59.
——"Birds of Ohio," Ohio State Acad. of Sci. Sp. paper No. 6, 1903, 125.
——"Birds of Cedar Point, Ohio," Wil. Bul. 22, 1910, 29-30.
Judd, N. S. "The Prairie Horned Lark in Fairfield County, Conn.," Bird Lore 10, 1908, 129.
Klugh, A. B. "Observations on the Birds of Prince Edward Island," Can. Field Nat. 25, 1921, 58.
Knight, O. W. "The Horned Larks of Maine," Auk 14, 1897, 371-374.
——"Birds of Maine, 1906, 325.
Kumlien, L. and N. Hollister. "Birds of Wis.," Bul. Wis. Nat. Hist. Soc. 3, 1903, 84.
Langille, J. H. "Our Birds in Their Haunts," N. Y. 1892, 9-15.
Lattin, F. H. "Horned Lark; Nesting Habits in Orleans Co., N. Y.," Ornithologist and Oologist 6, 1881, 10-11.
Levy, F. "An Unusual Horned Lark Family," Bird Lore 22, 1920, 85-86.
Lewis, H. F. "Birds of the Labrador Peninsula in 1923," Auk 42, 1925, 84.
Loomis, L. M. "*Otocoris alpestris praticola* in Chester Co., S. C.," Auk 4, 1887, 255.
——"A Further Review of the Avian Fauna of Chester Co., S. C.," Auk 8, 1891, 56-58.
MacDonald, H. "Incubation Period of the Horned Lark," Auk 33, 1916, 435.
MacAtee, W. L. "The Horned Larks and Their Relation to Agriculture," U. S. Dept. of Ag. Biol. Surv. Bul. 23, 1905.
McIlwraith, T. "Bird Notes from Western Ontario," Bul. Nutt. Ornith. Club 8, 1883, 145.
——"Birds of Ontario," London, 1894, 271.
Mearns, E. A. "Arizona Mt. Birds," Auk 7, 1890, 256.
Merriam, C. N. "Remarks on Some of the Birds of Lewis County, Northern N. Y.," Bull. Nutt. Ornith. Club, 1878, 54-55.
——"Preliminary List of Birds Ascertained to Occur in the Adirondack Region, Northeastern New York," Bul. Nutt. Ornith. Club 6, 1881, 231.
Merrill, J. C. "Notes on the Birds of Fort Klamath, Oregon," Auk 5, 1888, 259-260.

Moore, Wm. H. "Prairie Horned Lark in New Brunswick," Ottawa Nat. 16, 1903, 226-227.

Mouseley, H. "Five Years' Personal Notes and Observations on the Birds of Hatley, Stanstead Co., Quebec, 1911-1915," Auk 33, 1916, 72.

——"The Breeding of the Prairie Horned Lark at Hatley, Stanstead County, Quebec," Auk 33, 1916, 261-286.

——"A Study of Subsequent Nestings After Loss of the First," Auk 34, 1917, 381-393.

——"The Singing Tree," Auk 36, 1919, 339-348.

——"Birds of Hatley, Stanstead Co., Quebec," Auk 41, 1924, 576.

Naumann, "Naturgeschichte der Vögel Mitteleuropas," 3, no date, 4.

Nelson, E. W. "Birds of Northeastern Illinois," Bul. Essex Inst. 8, 110.

Norton, A. H. "Birds of the Bowdoin College Expedition to Labrador in 1891," Proc. Portland Soc. Nat. Hist. 2, 1901, 139-158.

——"The Eastern Distribution of the Prairie Horned Lark: A Question of Evidence," Auk 23, 1906, 225-226.

Nuttall, T. "Manual of the Ornithology of the U. S. and Canada," 1832, 455-457.

Oberholser, H. C. "A Review of the Larks of the Genus *Otocoris*," Proc. U. S. Nat. Mus. 24, 1902, 301, 884.

——"Horned Larks," Bird Lore, 20, 1918, 345-349.

Park, A. F. "Breeding of the Horned Lark in Eastern New York," Bul. Nut. Ornith. Club 7, 1881, 177.

Parkhill, C. H. "Nesting of the Prairie Horned Lark in Vermont," Ornith. and Ool. 14, 1889, 87.

Peabody, P. B. "The Desert Horned Lark," Warbler 2, 1906, 20-27.

Poling, O. C. "Early Nesting of the Prairie Horned Lark in Illinois," Ornith. and Ool. 14, 1889, 86-87.

Reed, C. A. "Bird Guide, Land Birds East of Rockies," 1923, 53.

Rhoads, S. N. "Notes on Some of the Rarer Birds of Western Pa.," Auk 16, 1899, 311.

Ridgway, R. "Notes on Birds Observed at Mount Carmel, Southern Illinois, in the Spring of 1878," Bul. Nut. Ornith. Club 3, 1878, 165.

——"A Cat. of the Birds of Illinois," Ill. State Lab. Nat. Hist. Bull. 4, 1881, 183.

Samuels, E. A. "Ornithology and Oölogy, of New England," 1869, 281-282.

Saunders, H. "Manual of British Birds," London, 1899, 259-260.

Scott, W. N. D. "Notes on Birds Observed During the Spring Migration in Western Missouri," Bul. Nutt. Ornith. Club 4, 1879, 141.

Scott, W. L. "The Winter Passeres and Picariae of Ottawa," Auk 1, 1884, 160.

Sennett, G. B. "*Otocoris alpestris praticola* Breeding in Erie, Pa.," Auk 6, 1889, 198.

Seton, E. T. "The Birds of Western Manitoba," Auk 3, 1886, 321.

——"Bird Records from Great Slave Lake Region," Auk 25, 1908, 71.

Smith, E. A. "Birds of Montgomery Co., Va.," Auk 29, 1912, 518-519.

Smith, H. M. and P. W. "Additions to the Avifauna of Washington, D. C., and Vicinity," Auk 5, 1888, 148.

Soper, J. D. "Birds of Wellington and Waterloo Cos., Ontario," Auk 40, 1923, 501.

Sutton, George M. "Flocking, Mating and Nest-Building Habits of the Prairie Horned Lark," Wilson Bul. V, 34, N. S. 1927, 131-141.

Swain, J. M. "Prairie Horned Larks Nesting in Maine," Auk 17, 1900, 387-388.

Swainson and Richardson. "Fauna Boreali Americana," 2, 1831, 245.

Swales, B. H. "Prairie Horned Lark *(Otocoris alpestris praticola)* in Maryland in Summer," Auk 39, 1922, 568.

Taverner, P. H. "The Birds of Shoal Lake, Manitoba," Canad. Field Nat. 33, 1919, 13.

Terrill, L. M. "Changes in the Status of Certain Birds in the Vicinity of Montreal, P. Q.," Ottawa, Nat. 25, 1911, 59.

Todd, W. E. C. "Breeding of *Totanus solitarius* and *Otocoris alpestris praticola* in Western Pa.," Auk 8, 1891, 236.

Torrey, B. "The Prairie Horned Lark *(Otocoris alpestris praticola)* on Mount Washington, N. H.," Auk 22, 1905, 414-415.

Townsend, C. W. "Extension of the Breeding Range of the Prairie Horned Lark *(Otocoris alpestris praticola)* to the Eastern Coast," Auk 21, 1904, 81.

Townsend, C. W., and Allen, G. M. "Birds of Labrador," Proc. Boston Soc. Nat. Hist. 33, 1907, 277-428 (Review only, seen in Auk 24, 1907, 451-452.)

Townsend, C. W. "Courtship of Birds," Auk 37, 1920, 390.

——"A Breeding Station of the Horned Lark and Pipit on the Gaspe Peninsula," Auk 40, 1923, 85-87.

Widmann, O. "A Preliminary Catalogue of the Birds of Missouri," Trans. Acad. Sci. St. Louis, 1907, 17, 143.

Williams, R. S. "Upper Missouri River Birds," Auk 5, 1888, 15.

Wilson, A. "Am. Ornith.," 1, 1808, 85-87.

——"Am. Ornith.," 2, 1831, 218-221.

Wilson, G. "Birds of Bowling Green, Ky.," Auk 39, 1922, 237.

Wood, N. A., and E. H. Frothingham. "Notes on the Birds of the Au Sable Valley, Mich.," Auk 22, 1903, 49.

Woodruff, E. G. "Notes from Northwestern Conn.," Auk 22, 1905, 420.

——"*Otocoris alpestris praticola* Breeding Eudy, Shannon Co., Mo.," Auk 25, 1908, 202.

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Plate II. The Prairie Horned Lark, Male and Female.

Fig. 1. Male, side view.

Fig. 2. Male, front view.

Fig. 3. Female, side view.

Fig. 4. Female, front view.

PLATE II

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Plate III. Winter Activities of the Prairie Horned Lark.

Fig. 1. Winter home at Evanston, Ill.

Fig. 2. Tracks in the snow. Note the walking gait and the marks of the long hind spur.

Fig. 3. Tracks of a male Lark through deep snow to a February song post.

PLATE III

Fig. 2

Fig. 3

Plate IV. Winter Activities of Prairie Horned Lark (cont.), and the Lark Home in April.

Fig. 1. *Amaranthus* and tracks of the Lark made while feeding on its seeds.

Fig. 2. At Evanston, Ill. This area of about 90 acres had been, two or three years previously, a marsh, was then drained for a golf course, and after the Chicago Elevated built into the region, was subdivided into urban real-estate streets and blocks. This, in 1926, provided nesting sites for twenty-one located nests of the Prairie Horned Lark.

PLATE IV

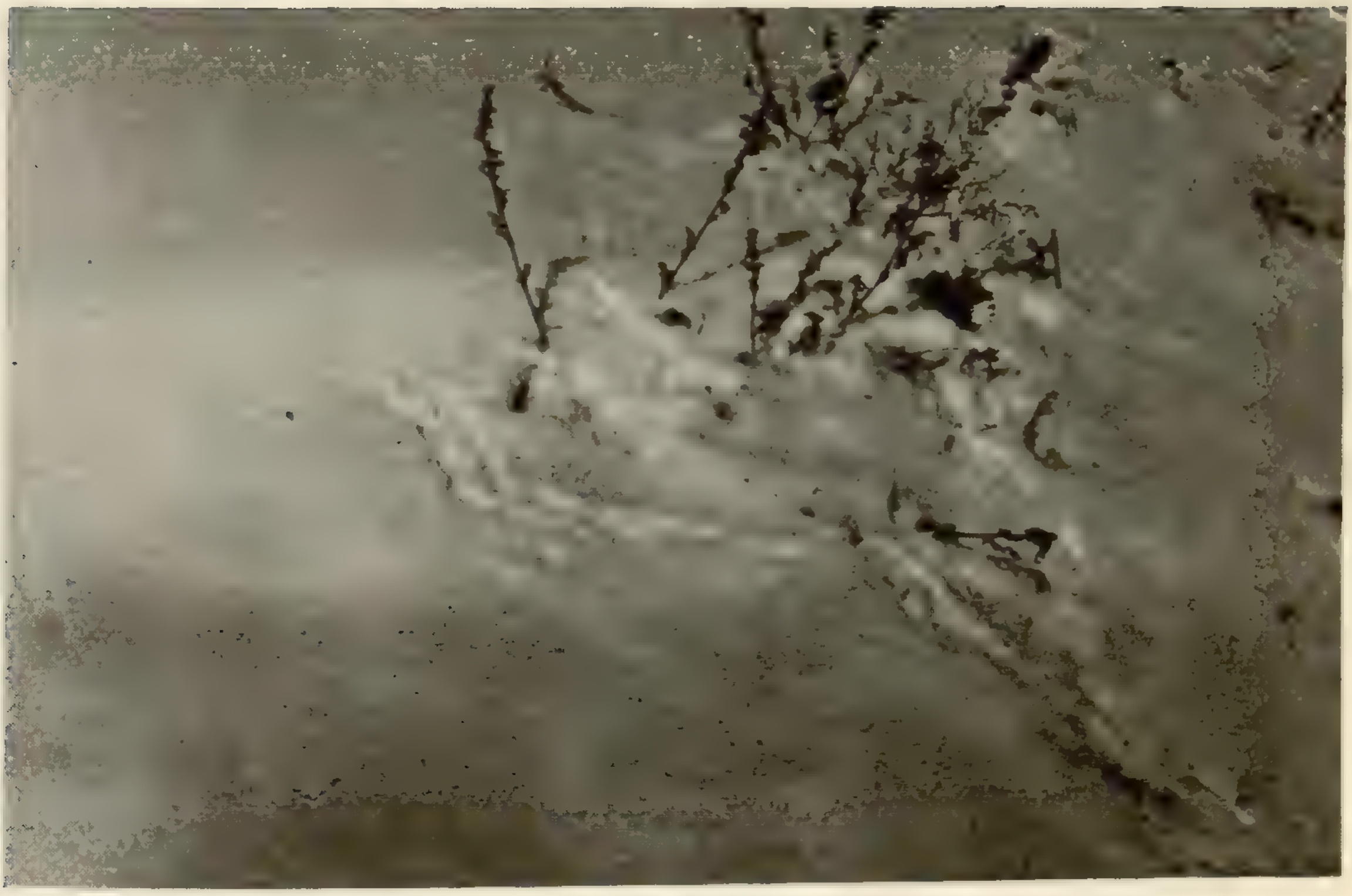

Fig. 1

Fig. 2

Plate V. Lark Home in April (cont.), and Nest Building.

Fig. 1. At Ithaca, N. Y. The last of the snow that destroyed the March nests of the Larks is still on the hills but renesting had begun (April 6).

Fig. 2. A newly dug excavation for a nest between two tufts of fall wheat.

PLATE V

Fig. 1

Fig. 2

Plate VI. Nest Building—continued.

Fig. 1. A nest nearly completed. Note the material thrown out in making the excavation and the two items (pebbles) of "paving" that have been carried in.

Fig. 2. An excavation under a clod beset with dead tufts of timothy. Note the few items (clods) of "paving".

Fig. 1

Fig. 2

Plate VII. Nest Building (cont.), and a March Nest.

Fig. 1. A nest (that of Fig. 2, Plate VI) nearly completed. An extensive "paving" has been placed about the border of the nest away from the dead grass protection. All of the material here shown was laid within twenty-four hours.

Fig. 2. Nest (A_1), surrounded and partially covered by snow on March 26 at Ithaca, N. Y. The female flushed as the nest was approached and snow tumbled into the cavity to melt partially from the warmth of the nest. Tracks, leading off from the lower edge, show that the Lark returned to the nest during an interval of the writer's absence.

PLATE VII

Fig. 1

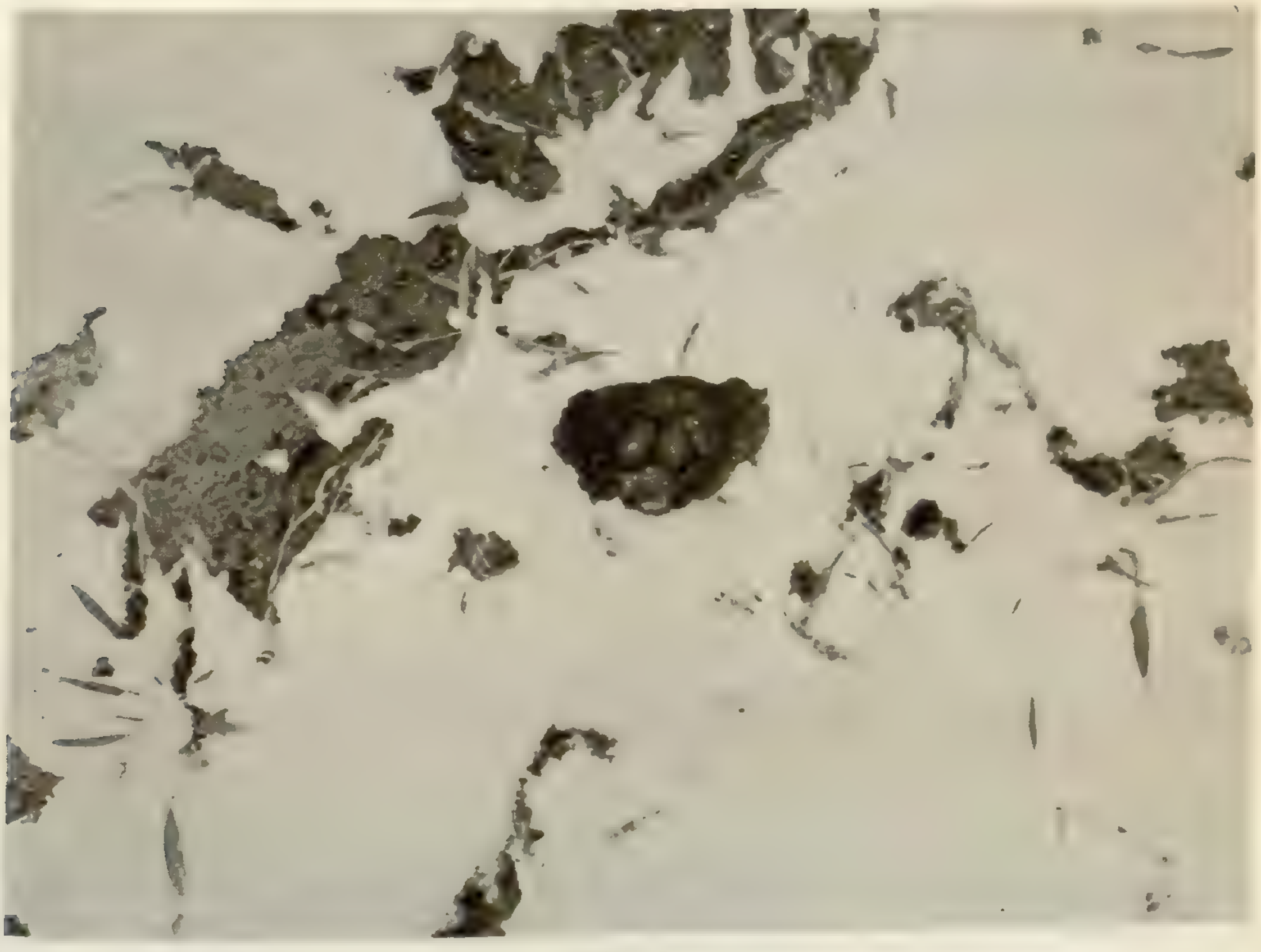

Fig. 2

Plate VIII. March Nests—continued.

Fig. 1. This nest, (B_1), at Ithaca, N. Y., was begun during the first mild weather of March, about the 11th or 12th. The eggs hatched March 28th, the young died of exposure March 31st and were buried under six inches of snow the next day. The nest is partially beneath a clump of fall wheat on the west. A small "paving" (pebbles) leads off to the north.

Fig. 2. Nest destroyed by late Marchsnows at Evanston, Ill., 1926.

Fig. 1

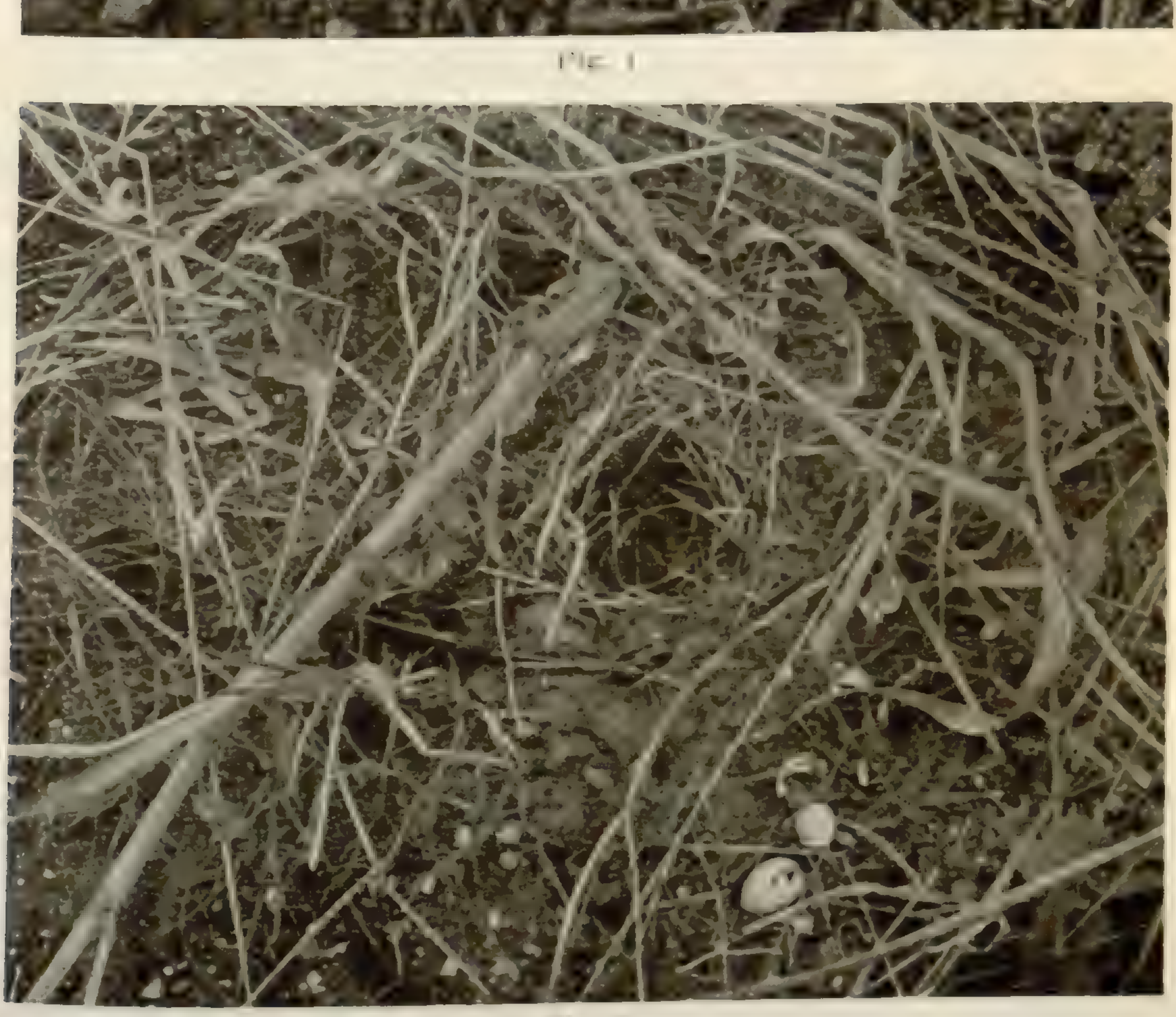

Fig. 2

Plate IX. April Nests.

Fig. 1. Fall wheat habitat of nest B_2 at Ithaca, N. Y.

Fig. 2. Nest B_2, April 15, 1927. Note that one egg is peculiarly marked. A later nest of this bird had a similarly marked egg (see Plate XVIII, Fig. 2).

PLATE IX

Fig. 1

Fig. 2

Plate X. April Nests—continued.

Fig. 1. The habitat of nest D, at Ithaca, N. Y., the overturned sod of a former meadow.

Fig. 2. Nest D, April 17, 1927. An overturned bit of sod with a tuft of dead grass is on the northwest, a "pavement" of clods extends to the south.

PLATE X

Fig. 1

Fig. 2

Plate XI. April Nests—continued.

Fig. 1. Nest No. 3 in the dead and sparse grass and weed stuff along the streetway in a real-estate subdivision at Evanston, Ill., April 23, 1926.

Fig. 2. Nest No. 5 built in the streetway of a real-estate subdivision at Evanston, Ill., with bare ground extending off to the south and east and a protection of dead thistle leaves (*Cirsium arvense*) and dead red-top grass (*Agrostis palustris*) on the northwest. Note the elaborate "pavement" of clods bordering the open sides (April 22, 1926).

PLATE XI

Fig. 1

Fig. 2

Plate XII. April Nests—continued.

Fig. 1. The streetway habitat which, in a single subdivision of about 90 acres near Evanston, Ill., provided suitable conditions for fourteen located nests of the Prairie Horned Lark in 1926. The nest in this photograph is in the inner angle formed by the two boards in the lower right-hand corner.

Fig. 2. Nest No. 7, April 22, 1926. A near view of the nest located by the boards in the habitat photographed above. Note the clod "pavement" laid along the board on the southwest margin of the nest. Dead *Agrostis palustris* surrounds the nest, a higher tuft of which is on the northeast. New spears of this grass are appearing here and there.

PLATE XII

Fig. 1

Fig. 2

Plate XIII. April Nests—continued.

Fig. 1. The habitat of nest No. 12 within a lot of the real-estate subdivision at Evanston, Ill., April 25, 1926. The nest location may be seen in the center foreground. The short, dead grass is blue grass (*Poa pratensis*).

Fig. 2. The habitat of nest No. 9, April 17, 1926, in the streetway of the subdivision at Evanston, Ill. The nest is in the outer edge of the dead grass clumps of *Agrostis palustris* in the center ground.

PLATE XIII

Fig. 1

Fig. 2

Plate XIV. April Nests—continued.

Fig. 1. Nest No. 9, April 17, 1926, in the outer edge of the street-way grass strip (see Fig. 2, Plate XIII). A "pavement" of clods can be seen along the east margin of the nest opposite the protecting tuft of *Agrostis palustris* on the west. New leaves of yarrow (*Achillea millefolium*) are appearing in the foreground.

Fig. 2. Nest No. 11, April 22, 1926, in bare, cracked soil thrown up by the laying of a sidewalk in the subdivision at Evanston, Ill.

PLATE XIV

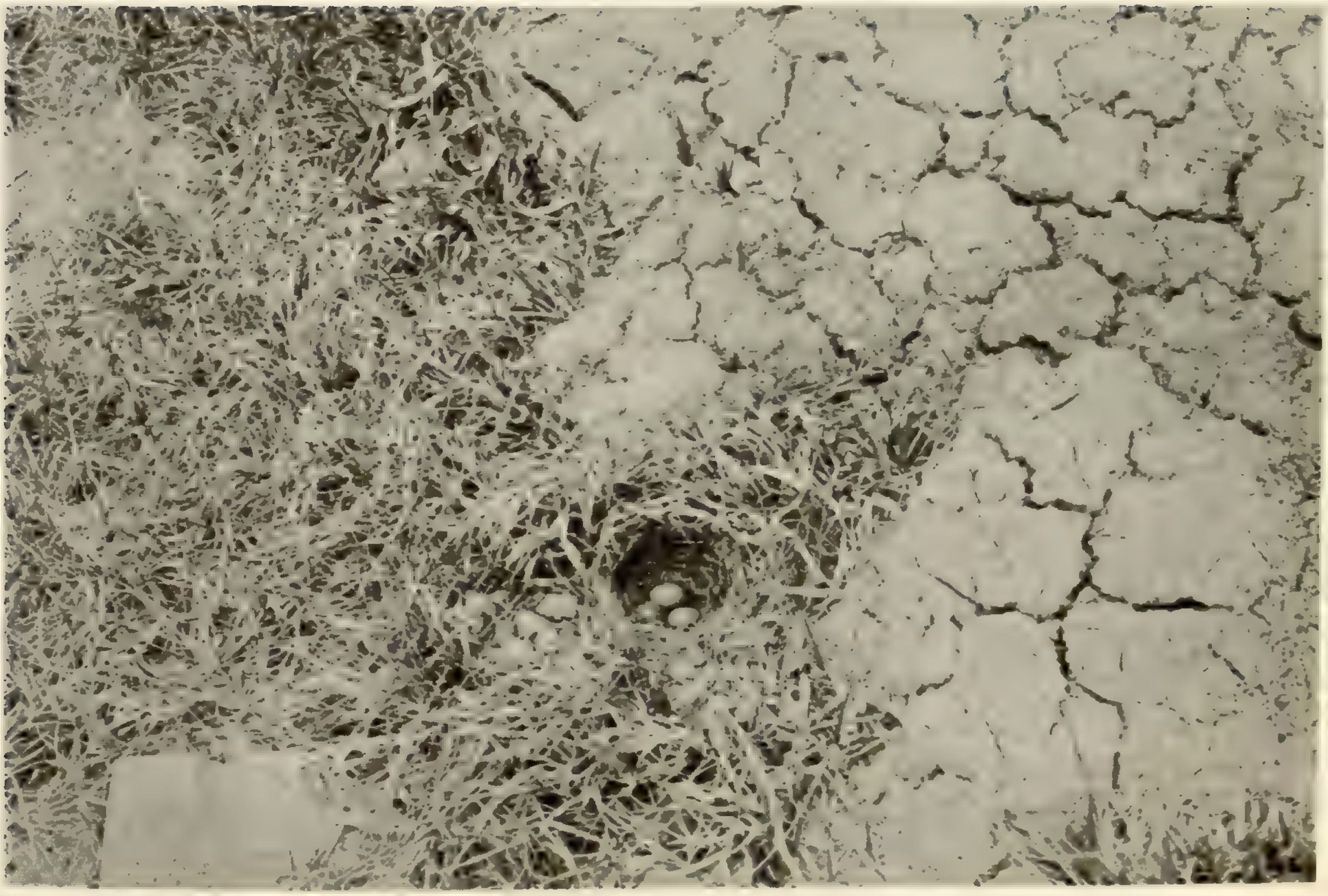

Fig. 1

Fig. 2

Plate XV. April Nests (cont.) and an Early May Nest.

Fig. 1. Nest No. 11 (see Plate XIV, Fig. 2), in near view. There is no protection near the nest—one of a very few exceptions to a general rule.

Fig. 2. Nest No. 15, May 5, 1926, in a streetway of the Evanston, Ill., subdivision. A dead tuft of *Agrostis palustris* arches over the north and west side, new blades of which have attained considerable length just behind. Between the old stems of primrose (*Oenothera biennis*) in front, an extensive clod "pavement" has been laid.

Fig. 1

Fig. 2

Plate XVI. A Late April Nest and a May Nest.

Fig. 1. Nest A_2, April 26, 1927, at Ithaca, N. Y. Fall wheat forms the protection on the north. This nest was built in the same territory as A, about eighty yards from the site of that earlier nest. One of the eggs here is unusually marked with black blotches at the larger end.

Fig. 2. Nest C between rows of fall rye at Ithaca, N. Y., May 3, 1927. The nest protection, a heavy weed-root, is on the southeast, the only case where the protection was not on the west, northwest or northeast. The eggs here have an unusually heavy ring of spotting about the larger end.

PLATE XVI

Fig. 1

Fig. 2

Plate XVII. May Nests (cont.) and a June Nest.

Fig. 1. Nest No. 14, May 4, 1926, in the streetway in the Evanston, Ill., subdivision. One of the very few nests of the Prairie Horned Lark without bare ground extending away from the front and without evidence of "paving." The grass is *Agrostis palustris*, dead blades of which arch over the nest on the north. New leaves of this grass are coming through the old.

Fig. 2. Nest No. 20, June 6, 1926, in the Evanston, Ill., subdivision. It contains two Cowbird and three Lark eggs, the only case of Cowbird parasitism in thirty-two observed nestings of the Prairie Horned Lark. New stems of *Agrostis palustris* surround the nest on the north and west; an old "pavement," beaten down by rain, extends to the southeast (right-hand side) and a dandelion plant (*Taraxacum officinale*) arises on the south.

PLATE XVII

Fig. 1

Fig. 2

Plate XVIII. June Nests—continued.

Fig. 1. Nest B_3 and habitat, June 9, 1927, at Ithaca, N. Y. The nest is in the center foreground. The tomato plants were set out after the nest was built.

Fig. 2. Nest B_3 in near view. On the west are stems of rye that the plow failed to turn under. The protection consists of two clods on the northwest. Note one egg with peculiar markings, a condition that existed in a former nest of this individual (see Plate IX, Fig. 2).

PLATE XVIII

Fig. 1

Fig. 2

Plate XIX. June Nests—continued.

Fig. 1. Habitat of nest No. 21, June 27, 1926, in the Evanston, Ill., subdivision. The nest is in the center ground, between the foreground and the nearer sidewalk.

Fig. 2. Nest No. 21, June 15, 1926. Young plants of the pasture ragweed (*Ambrosia artemisiaefolia*) surround the nest on all sides except the southeast. A clod "pavement" of this side has been obliterated by rain.

PLATE XIX

Fig. 1

Fig. 2

Plate XX. June and July Homes of the Prairie Horned Lark.

Fig. 1. The Ithaca home in June. The fall wheat of the center ground has forced the Larks to the cultivated garden areas of the foreground.

Fig. 2. To the few bare spots of this old vegetable garden west of Evanston, Ill., here given over to real-estate subdivision and weed-beset, the Larks were forced for the last of their nests in 1926 (July 10).

PLATE XX

Fig. 1

Fig. 2

Plate XXI. A July Home and Nest of the Prairie Horned Lark.

Fig. 1. Habitat of nest No. 22, July 10, 1926, in a deserted but subdivided vegetable garden at Evanston, Ill. The dominating weed is charlock (*Brassica arvense*). Beside a clumb of this, in the center ground, the nest was placed.

Fig. 2. Nest No. 22, July 8, 1926. On all sides but the southeast charlock (*Brassica arvense*) rises. When the nest was constructed, some three weeks earlier, the habitat was undoubtedly less weed-grown, more in keeping with Lark requirements.

PLATE XXI

Fig. 1

Fig. 2

Plate XXII. The Brooding Lark.

Fig. 1. Female brooding young of nest B_1, March 28, 1927, at Ithaca, N. Y.

Fig. 2. Female brooding young of nest No. 6, Evanston, Ill., April 25, 1927.

PLATE XXII

Fig. 1

Fig. 2

Plate XXIII. Nestling Prairie Horned Larks of Nest No. 7, Evanston, Ill. (see Plate XII, Figs. 1 and 2).

Fig. 1. Two recently hatched young, two eggs, April 26, 1926.

Fig. 2. Two young second day, two young first day, April 27, 1926.

Fig. 1

Fig. 2

Plate XXIV. Nestling Prairie Horned Larks of Nest No. 7—continued.

Fig. 1. Two young third day, two young second day, April 28, 1926.

Fig. 2. Young responding to whistle, April 28, 1926.

PLATE XXIV

Fig. 1

Fig. 2

Plate XXV. Nestling Prairie Horned Larks of Nest No. 7—continued.

Fig. 1. Two young fourth day, two young third day, April 29, 1926.

Fig. 2. Two young fifth day, two young fourth day, April 30, 1926. The younger nestlings are now noticeably smaller and are forced to occupy the back of the nest, the older and stronger thus are nearer the parents and the food which almost always approached over the boards and pavement (Fig. 1 of this plate is one of the few exceptions to this position).

Fig. 1

Fig. 2

Plate XXVI. Nestling Prairie Horned Larks of Nest No. 7—continued.

Fig. 1. Young responding to whistle, May 1, 1926. All still respond, though the eyes of the older are opening.

Fig. 2. Two young sixth day, two young fifth day, May 1, 1926. The discrepancy in size between the older and younger nestlings is here very noticeable, much more than the growth of one day (the difference in age), would account for if all had received the same amount of food.

PLATE XXVI

Fig. 1

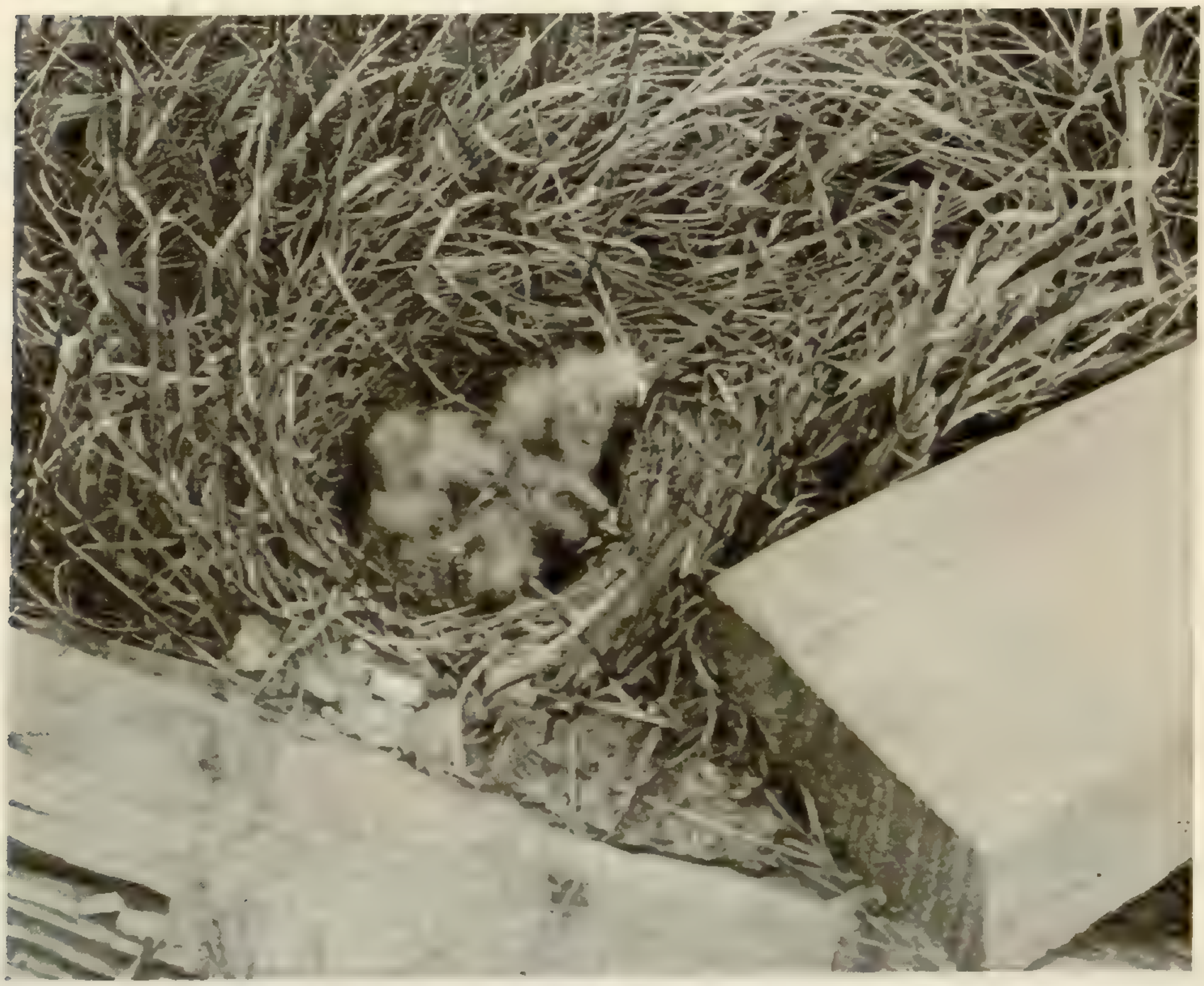

Fig. 2

Plate XXVII. Nestling Prairie Horned Larks of Nest No. 7—continued.

Fig. 1. Two young seventh day, one sixth day, May 2, 1926. The smallest died of starvation between this photograph and that of the preceding day. The sixth day bird remaining still responds to a whistle, whereas the seventh day young do not. The juvenile feathers of the seventh day birds are unsheathing.

Fig. 2. Two young eighth day, one seventh, May 3, 1926. Almost overnight the juvenile plumage unsheaths, the down begins to shed and the nestling changes entirely in aspect. The seventh day bird is pushed deeper into the rear of the nest.

PLATE XXVII

Fig. 1

Fig. 2

Plate XXVIII. Nestling Prairie Horned Larks of Nest No. 7 (cont.) and the Female Prairie Horned Lark Approaching Her Nest.

Fig. 1. Two young ninth day, May 4, 1926. Between this photograph and that of the preceding day the second of the two younger birds died of starvation, leaving two fully fledged nestlings shedding the last of their down.

Fig. 2. Female approaching nest B_1, Ithaca, N. Y., March 29, 1927, to brood young. The young are too chilled to respond at her approach. She has just swallowed an item of food brought for the young. They would not open their mouths for it. Note that she approaches the nest over the "pavement."

PLATE XXVIII

Fig. 1

Fig. 2

Plate XXIX. The Male Prairie Horned Lark in Care of the Nestlings.

Fig. 1. Male with excreta, on an old cabbage stump, by nest No. 22, July 10, 1926, at Evanston, Ill.

Fig. 2. Male at nest C_1, May 13, 1927, Ithaca, N. Y.

PLATE XXIX

Fig. 1

Fig. 2

Plate XXX. Daily Growth of the Prairie Horned Lark During the Nestling Period (Photographs of the Same Individual, from Nest No. 13, Evanston, Ill., except Fig 8, and Exactly One-half Natural Size).

Fig. 1. Egg.

Fig. 2. First day.

Fig. 3. Second day.

Fig. 4. Third day.

Fig. 5. Fourth day.

Fig. 6. Fifth day.

Fig. 7. Sixth day.

Fig. 8. Seventh day.

Fig. 9. Eighth day.

Fig. 10. Ninth day.

Fig. 11. Tenth day.

PLATE XXX

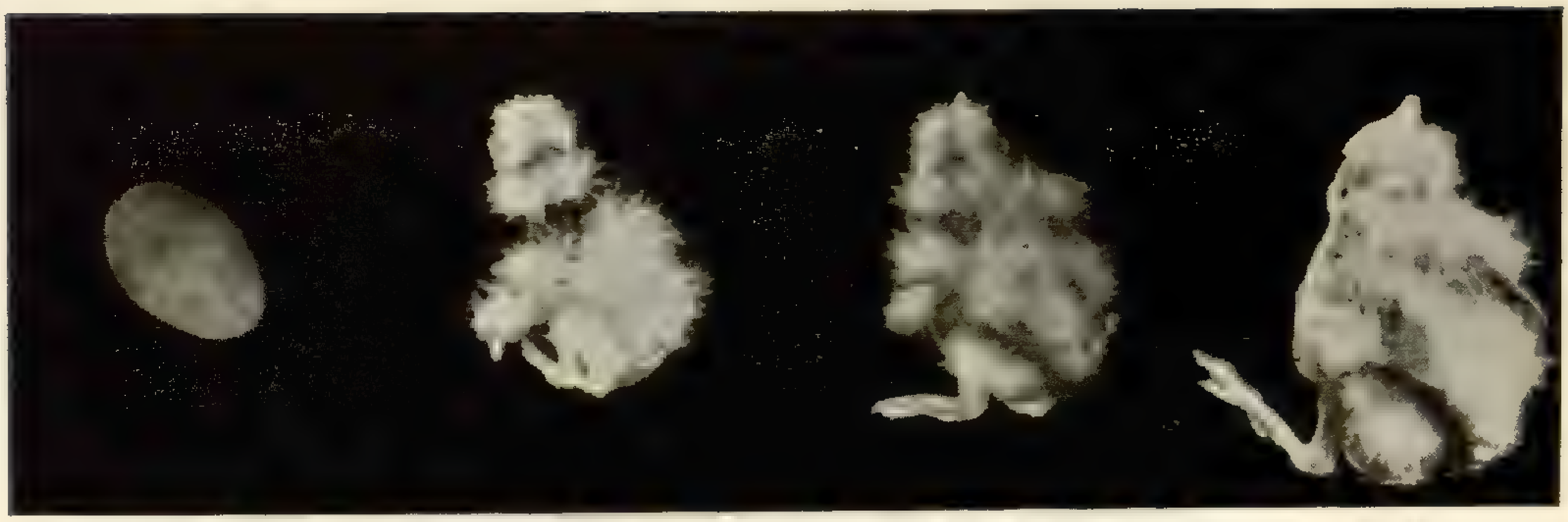

Fig. 1 Fig. 2 Fig. 3 Fig. 4

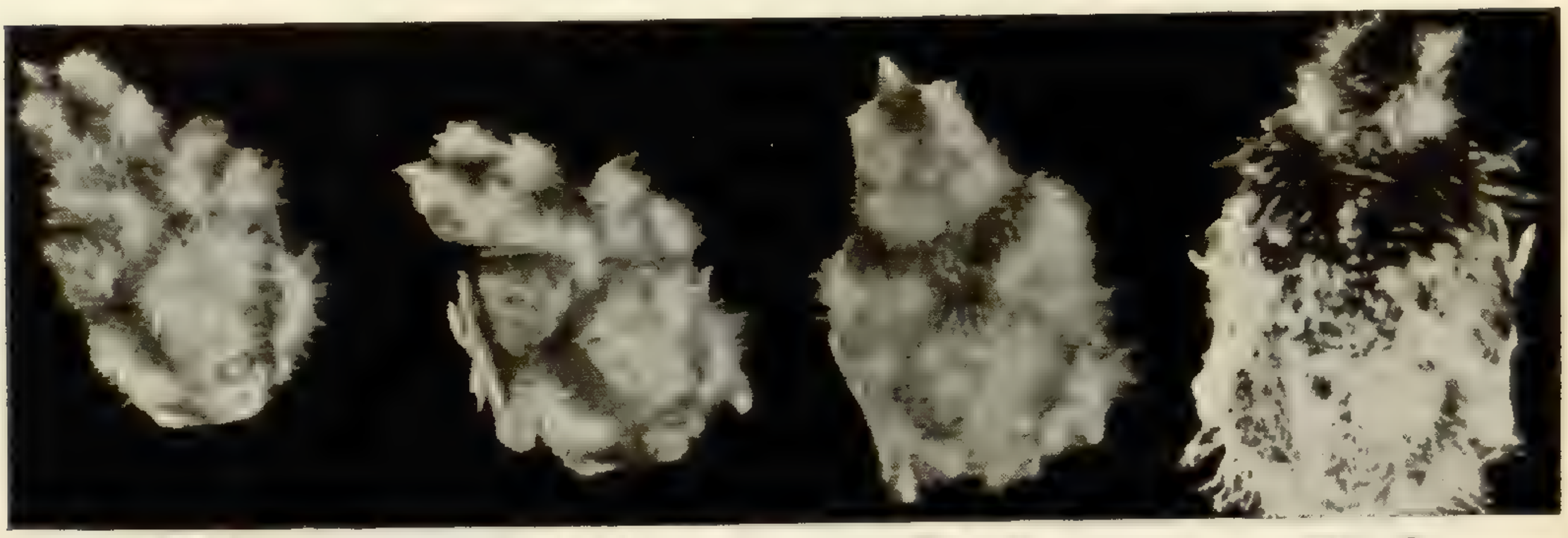

Fig. 5 Fig. 6 Fig. 7 Fig. 8

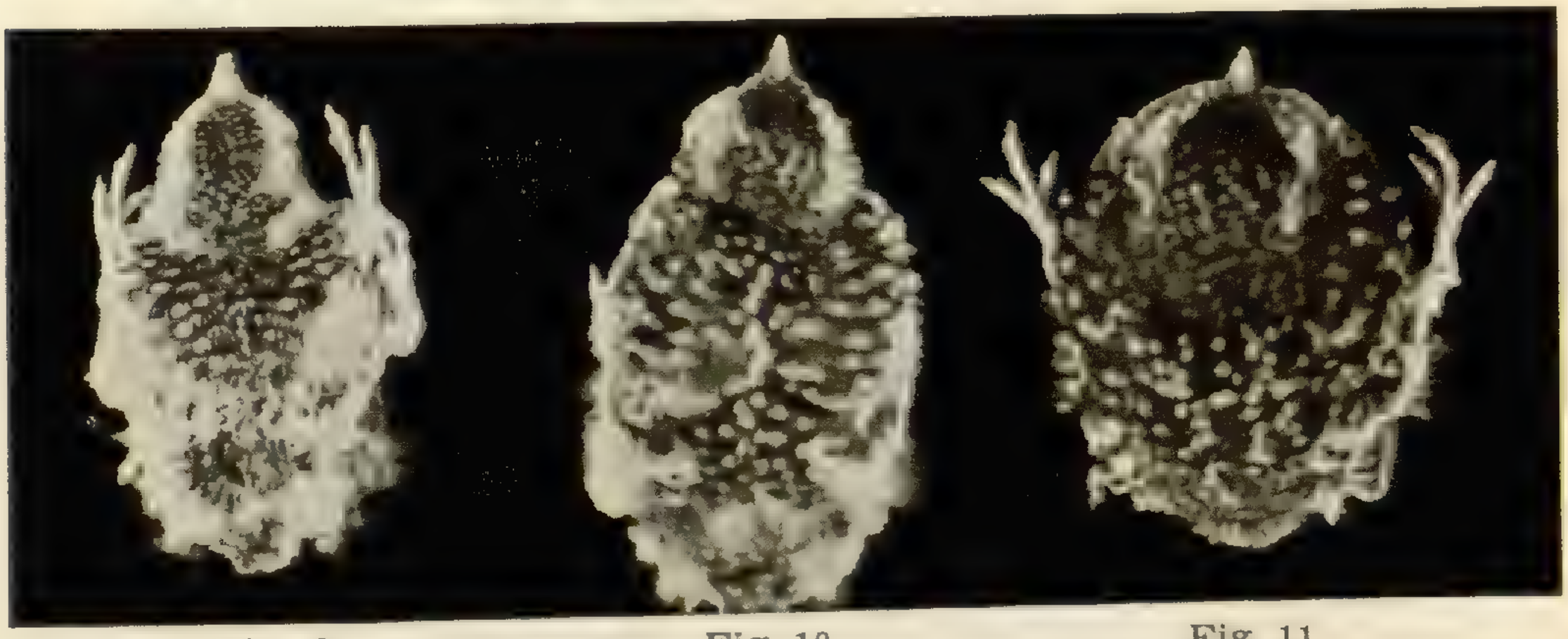

Fig. 9 Fig. 10 Fig. 11

Plate XXXI. Growth of the Nestling Prairie Horned Lark (cont.) and a Recent Nestling.

Fig. 1. Two young from the same nest (C_1, May 13, 1927, Ithaca, N. Y.) on the eighth day. The difference in their ages is a few hours only, but this difference is so vital in the matter of getting food from the parent that it frequently results in starvation of the younger. The smaller is retarded in size, feather growth and psychical development. Weight of larger 22.6 grams, of the smaller 11.5 grams.

Fig. 2. Young Prairie Horned Lark just after nest-leaving, July 11, 1926 (nest No. 22, Evanston, Ill.).

PLATE XXXI

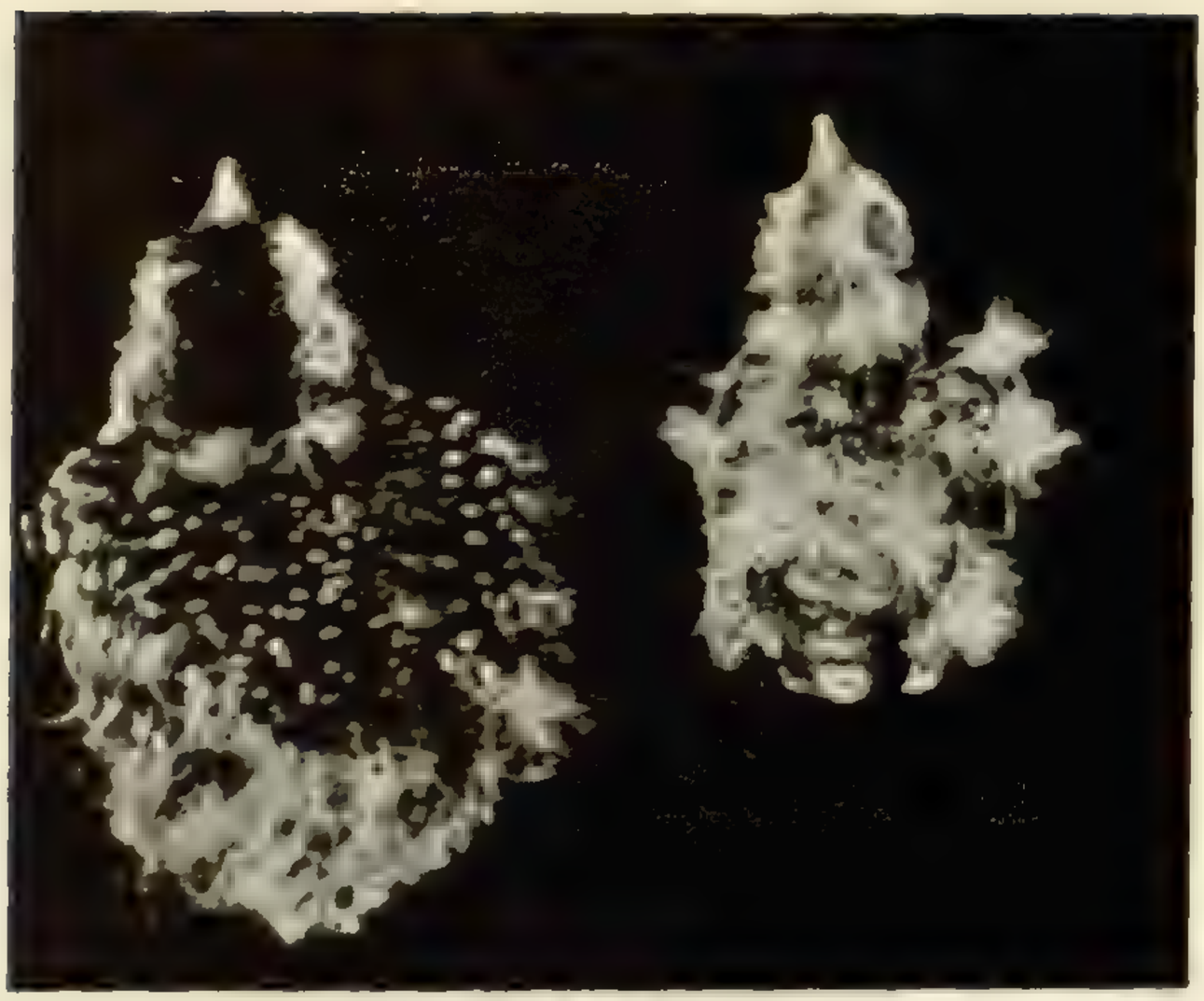

Fig. 1

Fig. 2

Plate XXXII. The Cowbird and the Prairie Horned Lark of Nest No. 20, Evanston, Ill.

Fig. 1. Cowbird, first day, (left); Lark, second day, June 9, 1926.

Fig. 2. Lark, third day, (left); Cowbird, second day, June 10, 1926.

Fig. 3. Lark, eighth day, (left); Cowbird, seventh day, June 15, 1926.

Fig. 4. Cowbird, ninth day, (left); Lark, tenth day, June 17, 1926.

Fig. 5. Lark (left), and Cowbird in nest the day prior to nest-leaving, June 17, 1926. Note the advanced plumage of the Lark as compared with the Cowbird.

PLATE XXXII

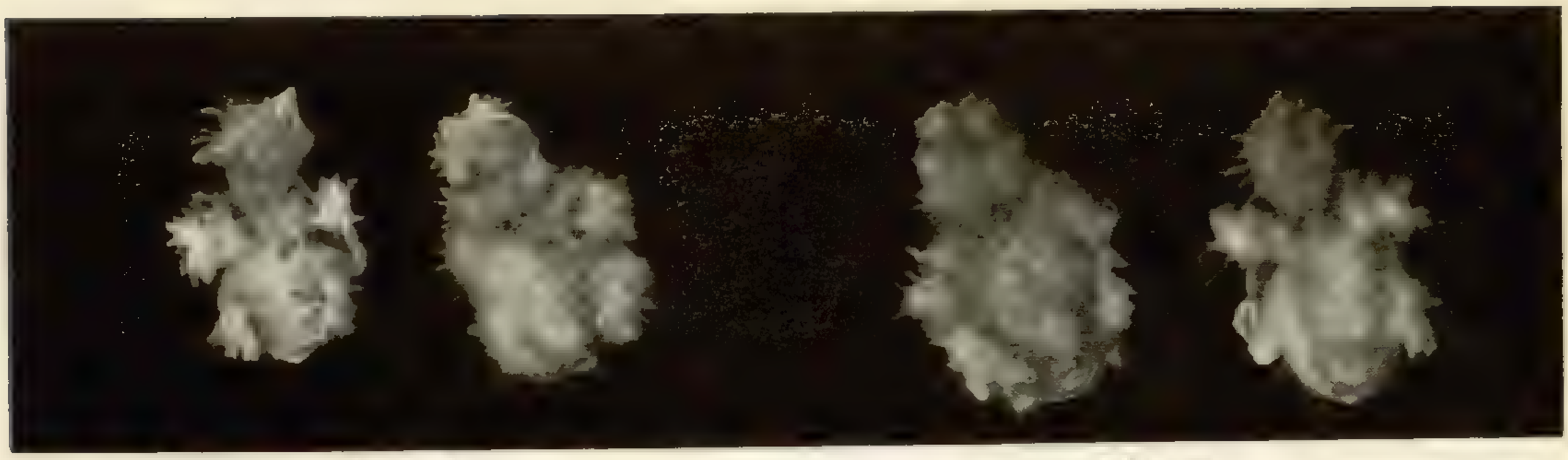

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Plate XXXIII. Concealing Coloration of Prairie Horned Lark Nestlings.

Fig. 1. The blending of natal down with nest surroundings (nest No. 13, May 7, 1926, Evanston, Ill.).

Fig. 2. "Picture pattern" of light and dense shadows of the ground in the juvenile plumage of young near nest-leaving (nest No. 4, May 3, 1926, Evanston, Ill.).

PLATE XXXIII

Fig. 1

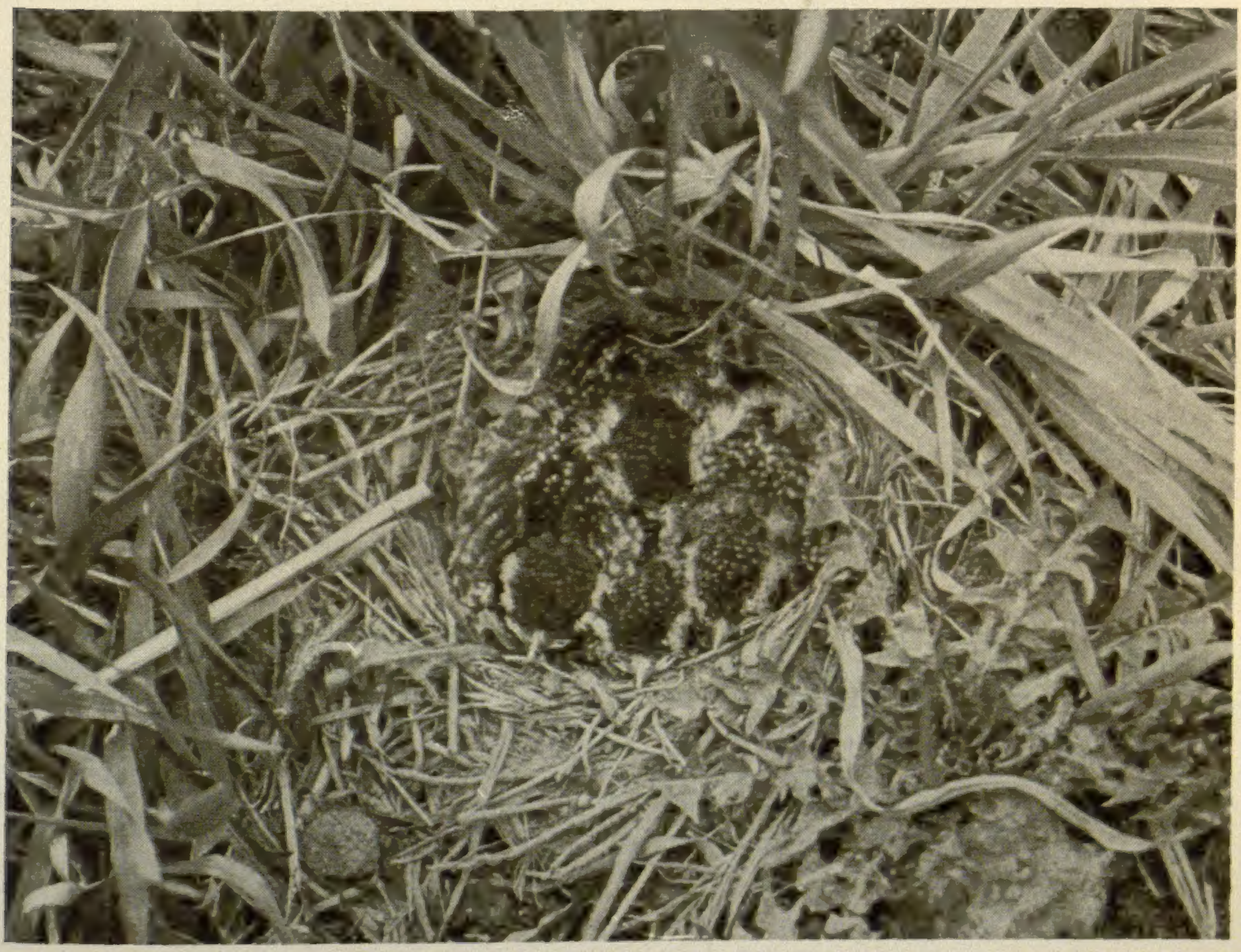

Fig. 2

Plate XXXIV. Concealing Coloration of Young Prairie Horned Larks.

Fig. 1. Recent nestling in "crouch-concealment" in short, sparse grass. The young Larks are semi-precocial in that they leave the nest three to four days before they fly. For their protection they have a mottled juvenile plumage that is an ideal "picture pattern" of their environment. Furthermore, they have developed a crouch-concealment, as have shore birds, and are always quiet when the adults are not near.

Fig. 2. Recent nestlings in "crouch-concealment" on bare, cracked ground.

PLATE XXXIV

Fig. 1

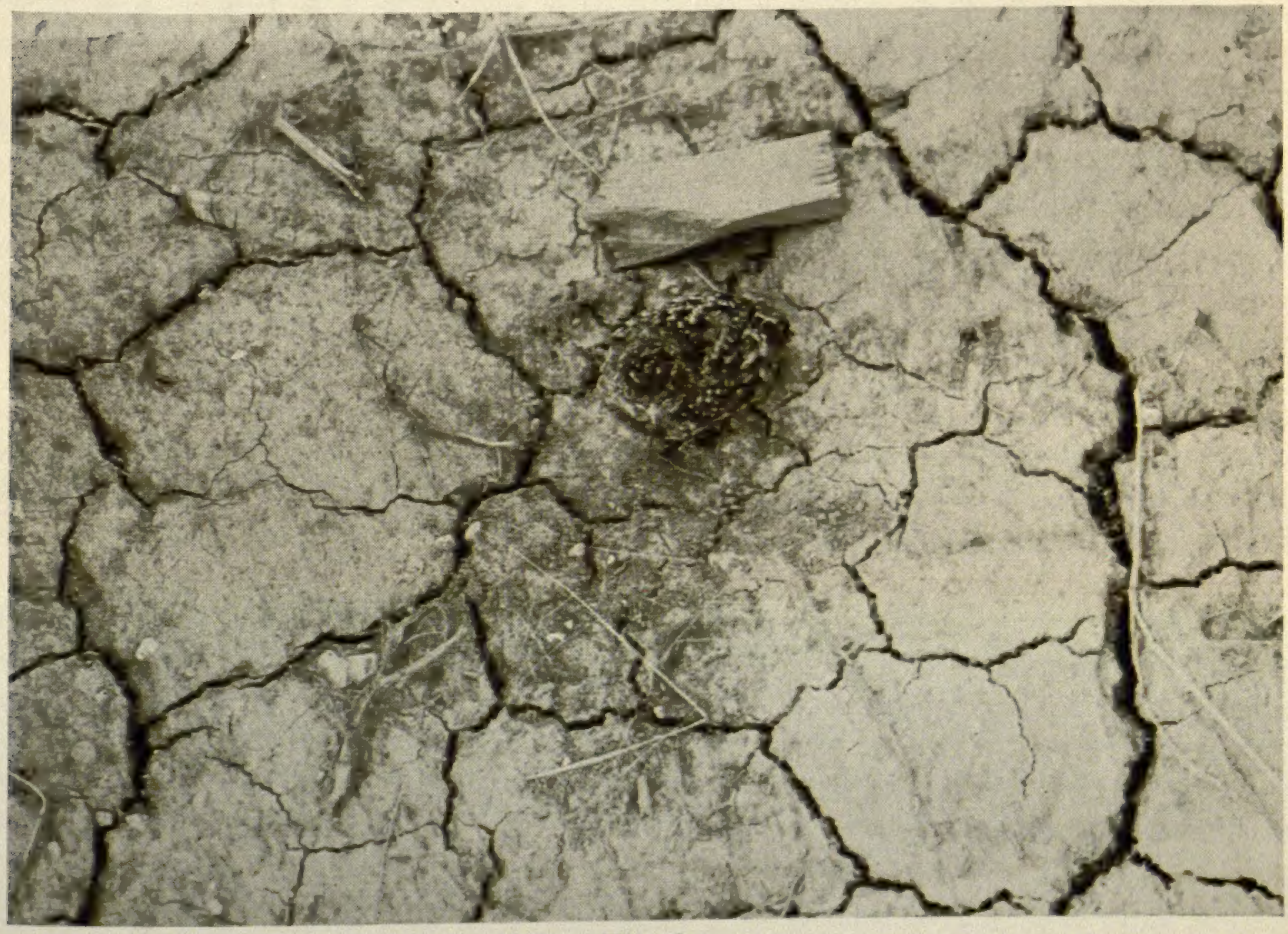

Fig. 2

Ornithological Contributions to the Transactions

With Prices of Available Papers

Preliminary Catalogue of Birds of Missouri.

By Otto Widmann. XVII, 289 p. Nov. 16, 1907.....$3.00

Birds of the Kansas City Region.

By Harry Harris. XXIII, 8, 160 p. Vol. XXIII, Feb. 27, 1919. Out of print.

Extracts from the Diary of Otto Widmann.

Nesting Habits of the Purple Martin. How Young Birds Are Fed. Where the Martins Roost.

The Crow's Winter Roost at St. Louis.

Our Birds in Winter.

Chaetura Pelagica (Linn.), Chimney Swift.

Birds of the Ozarks, Reminiscences of a Visit to Branson and White River, Spring of 1906.

By Otto Widmann. XXIV, 8..... .65

The Prairie Horned Lark.

By Dr. Gayle B. Pickwell. XXVII, ... p., ... pls., ... charts. ....., 1931..... 2.00